UC Santa Cruz
UC Santa Cruz Electronic Theses and Dissertations

Title

Movement energetics across landscapes: A canid case study

Permalink

https://escholarship.org/uc/item/13q463p7

Author

Bryce, Caleb M.

Publication Date

2017

Copyright Information

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

MOVEMENT ENERGETICS ACROSS LANDSCAPES:
A CANID CASE STUDY

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

By

Caleb Matthew Bryce

March 2017

The Dissertation of Caleb M. Bryce is
approved:

_____
Professor Terrie M. Williams, Chair

_____
Professor James A. Estes

_____
Professor Christopher C. Wilmers

_____
Professor Peter T. Raimondi

_____
Tyrus Miller
Vice Provost and Dean of Graduate Studies

TABLE OF CONTENTS

5 Synthesis   **134**

Bibliography   **140**

List of Tables

List of Figures

Abstract

Movement energetics across landscapes:

A canid case study

by

Caleb M. Bryce

Members of the family *Canidae* (e.g. foxes, coyotes, wolves, dogs) are among nature's most elite endurance athletes. To support their cursorial lifestyles, large canids achieve aerobic metabolic rates nearly three times those of similarly sized mammals and can play crucial roles in the structure and function of ecosystems. Fortunately, the field of animal energetics unites physiology and ecology by providing a common currency that links the performance of individuals to their interactions with the surrounding environment. Yet quantifying animal activity patterns and energy demand in the wild has been historically challenging, particularly for wide-ranging large canids. As a result, we are often left with in an incomplete understanding of the interplay between physiological and environmental factors driving movement, foraging, and ultimately population persistence in these species. In this dissertation, I present a laboratory-to-field approach for integrating behavioral and physiological data to forecast the resource demands required for survival by these highly mobile predators.

In my first data chapter (**Chapter 2**), I utilize biomechanics, kinematics, and energetics to quantify the effects of domestication and selective breeding on

locomotor gait and economy in canids, using several dog breeds as a model. I find that in addition to their close genetic and morphological ties to gray wolves, northern breed dogs have retained highly cursorial kinematic and physiological traits that promote economical movement across the landscape. Taking these lab-derived parameters into the field, in **Chapter 3** I investigate the impact of maximal performance parameters (e.g., speed, acceleration, maneuverability) on real-time chase outcomes of large canids and felids. Using hounds (as a proxy for wolves) to recapture pumas, I reconstruct pursuit and evasion tactics by each species to identify both physiological constraints and adaptive strategies that ultimately facilitate the coexistence of these species in the wild. Finally, in **Chapter 4** I measure free-ranging travel patterns and their costs in Alaskan wolves over 8 months after calibrating accelerometer- and GPS (Global Positioning System)-equipped collars on captive conspecifics. I demonstrate that activity and energy expenditure in wolves is highly varied across the Denali National Park & Preserve, reflecting regional habitat and prey heterogeneity.

Ultimately, these chapters provide novel insight into how the elevated energetic demands of canids influence their ability to structure the ecological communities they inhabit. Although the drivers of activity and predation by canids are complex, the results of this work demonstrate the capability of animal-born technology to identify instantaneous to seasonal-scale patterns in energy expenditure and its role in shaping moving ecology and species interactions.

To the memory of Mary Zavanelli,

(1955-2017)

who meant so much to so many.

She will remain an inspiration for all of us

privileged enough to know her.

Acknowledgements

This dissertation[1] is a testament to the power of friendship and collaboration. I had the gracious assistance of so many people over the course of my graduate career, but those I mention here are the main links in a vast support network.

First and foremost, my graduate advisor, Dr. Terrie Williams, could not have been more inspiring or positive to work alongside. She went out on a limb to welcome me into her lab on straight out of college (i.e. I had no MS degree or even clear direction for my PhD!). It was particularly risky since I wasn't even pursing a diving physiology project (the bread and butter of our lab), but rather wanted to work with terrestrial carnivores…using novel technology to boot! Terrie, how can I adequately thank you for the opportunities you gave me to find the pulse on wild lions in Kenya, or smell the fishy breath of Weddell seals in Antarctica? Through those and so many other experiences, you've shown me how being a comparative animal physiologist can mean so much more than being confined to a sterile laboratory. You've been the wind under my wings in graduate school, granting me the freedom and support to forge interdisciplinary collaborations and travel repeatedly across the globe for cutting-edge conservation research. Thanks for further instilling

---

[1] The text of this dissertation includes a reprint of the following previously published material: Bryce, C.M. and Williams, T.M. (2017). Comparative locomotor costs of domestic dogs reveal energetic economy of wolf-like breeds. *Journal of Experimental Biology*. 220 (312-321). The co-author listed in this publication was directly involved with the development of my first data chapter (Chapter 2). For chapter 2, C.M.B. and T.M.W. conceived and designed the study. C.M.B. and T.M.W. conducted all experiments. C.M.B. analyzed the data and wrote the manuscript with editorial advice provided by T.M.W.

within me a passion for saving species from extinction, and giving me the skills to start doing so!

My other dissertation committee members (Jim Estes, Pete Raimondi, and Chris Wilmers) were also instrumental in the successful completion of this PhD research. Jim, thank you for showing me that a world-renowned, brilliant scientist can still be humble and down-to-earth, and for helping me think more "out of the box" about broad-scale ecological patterns and their implications. Pete, I always appreciated your prompt feedback and insightful comments on during our annual meetings. Your ability to effectively communicate complicated statistics is remarkable and appreciated! Chris, thank you for informally adopting me into your lab and the puma project in Santa Cruz. Your inclusivity and willingness to join me for mountain bike rides to talk about analytical crises with R code (among other things) were very appreciated.

My collaborators each deserve a sincere thank you. For Chapter 2, thanks to all the dog owners, as well as D. Sur, C. Hill, C. Casey, C. Reichmuth, T. Kendall and B. Richter for dog handling and training assistance. For Chapter 3, thank you California Dept. of Fish and Game, P. Houghtaling, D. Tichenor, T. Collinsworth, O.P. Dewhirst, L. McHuron, B. Nickel, and several undergraduate field assistants for their significant field support during hound-assisted puma recaptures. The captive and wild wolf fieldwork (Chapter 4) was the icing on the cake of my dissertation research. At Wolf Park, Dana Drenzek took me under her wing and gave me incredible hands-on encounters with 10 captive wolves during the wildlife collar calibration. She also

assembled a team of volunteers to help train the wolves for my project, so thank you all. In Denali, Steve Arthur, Bridget Borg, and the staff at the Park Headquarters welcomed me with open arms and a warm office in the minus 40° weather of interior Alaska in early March. I owe a great deal of gratitude to the skilled and fearless pilots (T. Cambier & S. Hamilton) and wolf ski team (D. Savage, C. Harrington, E. McClellan, and A. Christopherson). Your devoted effort to help me deploy the accelerometer-GPS collars was the linchpin in the whole dissertation coming together, which came off without a hitch. Thank you for being collaborators, colleagues, and friends in the challenging field of managing contentious wildlife.

Nearly six years ago, I had the privilege of joining a terrific group of people: the Williams Lab (Dr. Terrie Williams and during my time, Dr. Robin Dunkin, Dr. Shawn Noren, Dr. Jen Maresh, Dr. Nicole Thometz, Anthony Pagano, and Jason John). Collectively, we custom-designed lab equipment for various projects, spent weeks (cumulatively!) reading and editing one another's proposal and manuscript writing, listened to innumerable practice talks for conference and job interviews, and saved stranded marine mammals when the opportunities arose. I'm forever grateful for such a great group of colleagues and friends to do science with! The same goes for cohort 2011. All 8 of us have now successfully completed graduate school (who would have thought?), and I couldn't be more privileged to share the journey with you. Thank you as well to staff and friends in EEB, ENVS, and around Santa Cruz, CA. You've made living and working here a fantastic experience for Carli and I.

Mike Mooring, my undergraduate advisor at Point Loma Nazarene University, remains a steadfast pillar of life, faith, and career goals. Mike almost single-handedly inspired my passion for large carnivore research and conservation, first in his classroom, then in the cloud forests of Costa Rica. Over the last 10 years, we've stayed in touch and the Mooring family's open door policy for talking about anything and everything has left an indelible mark on how Carli and I offer hospitality. Thank you!

My family (immediate and extended) could not have been more supportive of Carli and I as we voyaged through Santa Cruz, and wherever else graduate school took us. Thank you, Mom and Dad, for trusting me at every turn and giving me the freedom to spread my wings. Your loving support has been unwavering and was often the unspoken backbone of this dissertation endeavor. Tim and Jennie, thank you is inadequate for giving me your daughter in marriage midway through graduate school. You clearly love and trust me too, and I couldn't be married in to a better extended family!

Last but certainly not least: Carli Allison Coco. You're my best friend, my partner in crime, my adventure buddy, and the love of my life all in one. How could I ask for more? You've been right by my side through the thick and thin of graduate school, from kissing giraffes in Africa to repeatedly reviving me after forgoing food and sleep to work, and everything in between. You signed up for the package deal, and you got it! Thank you from the bottom of my heart. I'm so thrilled for the road that lies ahead, wherever it may take us!

CHAPTER 1

Introduction

For every organism, metabolic energy is critical for fueling each of life's processes (e.g. maintenance, digestion, growth, locomotor activity, thermoregulation, developmental and reproductive state). As the currency of ecosystem function, energy demand ultimately underlies the behavioral decisions animals make, driving where and how often they feed (Stephens & Krebs 1986; Speakman 2000; Brown et al. 2004; Humphries & McCann 2014). As a result, an animal's ability to balance its energetic budget has direct consequences for both its daily survival and lifetime fitness (Kleiber 1961; McNab 2002; Withers *et al.* 2016a).

Energy demands are particularly elevated in large mammalian carnivores, given the compounding effects of body size, (Peters 1983), endothermy (Bennett & Ruben 1979), and carnivory (Carbone, Teacher & Rowcliffe 2007; Carbone, Pettorelli & Stephens 2011) on metabolism. Furthermore, because terrestrial locomotion is expensive, the metabolic costs associated with movement can account for substantial portions of large carnivore daily energy budgets (Schmidt-Nielsen 1972; Garland 1983; Karasov 1992; Gorman *et al.* 1998; Steudel 2000; Girard 2001;

Weibel *et al.* 2004; Rezende *et al.* 2009; Scantlebury *et al.* 2014). These high

energetic constraints translate into substantial resource requirements for large

carnivores, which must patrol expansive territories in order to encounter sufficient

vulnerable prey (Carbone *et al.* 1999; Ripple *et al.* 2014). Understandably,

deciphering the free-ranging activity patterns and associated energy budgets for these

animals has been difficult.

Given their wide-ranging and highly active lifestyles, members of the family

Canidae (e.g. foxes, dogs, coyotes, wolves; canids hereafter) are quintessential

persistence predators. Canids are hypercursorial hunters, having specialized

morphological and physiological adaptations for aerobic running (reviewed in Taylor,

Weibel & Karas 1987). With the highest sustained metabolic rates on record

(Hinchcliff et al., 1997), both domestic and wild canids are considered among

nature's most elite endurance athletes (Snow 1985; Poole & Erickson 2011; Miller *et

al.* 2015). Indeed, *Canidae* members exhibit aerobic performance capacities roughly

three times greater than those of equivalently sized terrestrial mammals (Seeherman

et al. 1981; Weibel *et al.* 1983; Weibel, Taylor & Richard 1987; Weibel *et al.* 2004;

Weibel & Hoppeler 2005). This unprecedented ability of canids to utilize oxygen for

locomotor activity enables them to run for extended periods at sustained speeds

without becoming anaerobic (Okarma & Koteja 1987; Koteja 1987).

For the largest wild canid, the gray wolf (*Canis lupus*), survival depends on

roaming widely on a daily basis to locate, pursue, and kill fleeing prey (Mech 1970;

Macdonald & Sillero-Zubiri 2004; Mech, Smith & Macnulty 2015a). The drive for

predation in wolves can trigger significant and cascading influences that propagate broadly to other species (reviewed in Ripple *et al.* 2014), a phenomenon documented across a wide range of ecosystems (Beschta & Ripple 2009). Moreover, wolves initiate both density and behaviorally-mediated trophic cascades by directly decreasing prey populations and indirectly impacting the behavior of herbivores (Ripple & Beschta 2004; Christianson & Creel 2014; Creel et al. 2015; Ripple, Beschta & Painter 2015) and sympatric mesopredators (Berger & Gese 2007; Levi & Wilmers 2012; Ripple *et al.* 2013; Newsome & Ripple 2014).

Because these effects propagate downward through food webs (Hairston, Smith & Slobodkin 1960; Paine 1980; Terborgh & Estes 2010), the abundance and distribution of wolves and other large carnivores often dictate the design of reserves and protected habitats (Noss *et al.* 1996; Carroll *et al.* 2003; Simberloff 2003; Ray *et al.* 2005; Estes *et al.* 2011; Ordiz, Bischof & Swenson 2013). Given the global decline in many of these keystone species (Morrison et al. 2007; Ripple et al. 2014; Di Minin et al. 2016), the quantification of free-ranging behaviors and resulting energy demands is integral for defining predator resource requirements and establishing critical habitats and corridors for conservation (Berger-Tal et al. 2011; Wilmers et al. 2013; Laundré 2014; Williams et al. 2014).

Despite wolves' keystone role in structuring ecosystems, their low densities, wide-ranging behavior, and general avoidance of human-modified landscapes has made measuring their fine-scale activities and prey demands a long-standing challenge (e.g. Mech & Boitani 2003; Ripple et al. 2014). To date, most estimates of

mammalian energetics have been coarse, cumulative values of field metabolic rate derived from doubly-labeled water studies over weekly timescales (Speakman 1997; Halsey 2011). Wild wolf metabolic rates (and hence prey demands) have been modeled and estimated based on basal metabolism (Weiner 1989; Glowacinski & Profus 1997; Peterson & Ciucci 2003), but rarely empirically measured (Swain, Costa, and Mech, cited in Nagy 1994). My dissertation research addressed this need by developing a laboratory-to-field approach for quantifying the detailed locomotor performance (e.g. speed, maneuvering), movement patterns (e.g. hunting, dispersal, den attendance), and associated energetic costs from wolves and other cryptic carnivores over instantaneous to seasonal timescales.

With the overarching goal of measuring free-ranging canid energetics across landscapes, in **Chapter 2** I used both laboratory and field-based techniques to investigate the exercise physiology of domestic dog breeds. As readily available wolf proxies, examining dogs enabled me to determine the potential effects of domestication and selective breeding on locomotor gait and economy in large canids. At preferred speeds, I compared gait mechanics, kinematics, and mass-specific metabolism of three large (>20 kg) dog breed groups (northern breeds, hounds, and retrievers) of varying morphological and genomic relatedness to their shared progenitor, the gray wolf. I show that the cost of transport (COT) and energy cost per stride during trotting and galloping were significantly lower for northern breed dogs relative to hounds and retrievers of comparable mass. These results suggest that, in addition to their close genetic and morphological ties to gray wolves, northern breed

4

dogs have retained highly cursorial kinematic and physiological traits that promote economical movement across the landscape.

Measuring fine-scale movement, performance, and energetics of large carnivores and their prey is critical for understanding the physiological underpinnings of trophic interactions. For **Chapter 3**, I took the laboratory-derived performance parameters of large canids (Chapter 2) and felids (Williams *et al.* 2014) into the field for a unique, opportunistic study during routine recollaring efforts with local pumas. I calibrated then deployed accelerometer and global positioning system (GPS)-equipped collars to monitor escape maneuvers and energetics during pseudo predator-prey chase sequences of trained scent hounds pursuing pumas that were simultaneously instrumented. By reconstructing real-time speed, turning performance, and energy demand for each species across 4 chases, I investigated how morphological and physiological constraints in the hunting modes of large canids and felids impact their maximal performance, chase strategies, and interaction outcomes. Pumas, with smaller relative heart masses and lung volumes, compensated for their inferior endurance capacity by utilizing terrain (e.g. escaping up steep, wooded hillsides) and evasive tactics (e.g. jumping into trees, running in a figure-8 pattern) during escapes. In contrast, pursuing hounds maintained faster average speeds and worked cohesively as a pack to tree each puma prior to anesthetization.

Over a much wider spatiotemporal scale, in **Chapter 4** I used similar animal-born technology to examine the behaviors, travel patterns, and daily energetic expenditures (DEE) of 5 adult male wolves over 8 months in Alaska's Denali

National Park and Preserve (DNPP). Spatial (GPS) data from an additional 14 concurrently monitored wolves (9 packs total) were used to assess how wolf movements and densities varied with habitat and prey heterogeneity along the northern extent of the Alaska Range. I found that wolves occupying habitat which supports salmon but few large ungulates (western DNPP) had the highest average DEE, the lowest within-pack wolf densities, and the smallest average pack size relative to central and eastern DNPP, which have access to more abundant ungulate populations. This suggests that encountering sufficient prey and maintaining energy balance may be more challenging for wolves in western DNPP. Ultimately, I used the observed activity patterns and DEE of wolves in each region to model seasonal, species-specific prey demands for packs of various sizes in each region of northern Denali.

Together, chapters 2, 3, and 4 demonstrate the utility and flexibility of the laboratory-to-field approach for gaining novel insights into difficult to observe species through advanced animal-born technology. In the final chapter (**Chapter 5**), I synthesize the findings from all three data chapters and discuss how this dissertation improves our understanding of large carnivore field physiology and resource requirements. I conclude by highlighting how the approach can serve as a powerful management and conservation tool for mitigating human-carnivore conflict and promoting the keystone role of apex predators in the fabric of the landscape.

CHAPTER 2

Comparative locomotor costs of domestic dogs reveal energetic economy of wolf-like breeds

Abstract

The broad diversity in morphology and geographic distribution of the 35 free-ranging members of the family *Canidae* is only rivaled by that of the domesticated dog, *Canis lupus familiaris.* Considered to be among nature's most elite endurance athletes, both domestic and wild canids provide a unique opportunity to examine the variability in mammalian aerobic exercise performance and energy expenditure. To determine the potential effects of domestication and selective breeding on locomotor gait and economy in canids, we measured the kinematics and mass-specific metabolism of three large (>20 kg) dog breed groups (northern breeds, retrievers, and hounds) of varying morphological and genomic relatedness to their shared progenitor, the gray wolf. By measuring all individuals moving in preferred steady-state gaits along a level transect and on a treadmill, we found distinct biomechanical, kinematic, and energetic patterns for each breed group. While all groups exhibited reduced total cost of transport (COT) at faster speeds, the total COT and net COT during trotting and galloping were significantly lower for northern breed dogs (3.0 and 2.1 J·kg^{-1}·m^{-1},

respectively) relative to hound (4.2 and 3.4 $J \cdot kg^{-1} \cdot m^{-1}$, respectively) and retriever dogs (3.8 and 3.0 $J \cdot kg^{-1} \cdot m^{-1}$, respectively) of comparable mass. Similarly, northern breeds expended less energy per stride (3.5 $J \cdot kg^{-1} \cdot stride^{-1}$) than hounds or retrievers (5.0 and 4.0 $J \cdot kg^{-1} \cdot stride^{-1}$, respectively). These results suggest that, in addition to their close genetic and morphological ties to gray wolves, northern breed dogs have retained highly cursorial kinematic and physiological traits that promote economical movement across the landscape.

Introduction

All domestic dogs (*Canis lupus familiaris*) are recent and exclusive decedents of gray wolves, *Canis lupus* Linnaeus, 1758, having been domesticated in the last 15,000-30,000 years (Freedman *et al.* 2014; Skoglund *et al.* 2015; Wang *et al.* 2016). However, among the nearly 400 breeds representing modern dogs (Kleiman, Geist & McDade 2003), unique artificial selection trajectories (Galibert *et al.* 2011; Jimenez 2016) have resulted in extreme morphological diversity that exceeds that for the remainder of the family Canidae (Wayne 1986, 2001; Wilcox & Walkowicz 1995; Clutton-Brock 1999; Lindblad-Toh *et al.* 2005; Vaysse *et al.* 2011). In recent years, much emphasis has been placed on elucidating the origins of dog domestication from genomic (e.g. Freedman et al., 2014; Parker, 2012; Skoglund et al., 2015; Vonholdt et al., 2010), to zooarcheological (Pionnier-Capitan *et al.* 2011; Perri 2016), morphometric (Drake, Coquerelle & Colombeau 2015), and biogeographical evidence (Larson *et al.* 2012) By comparison, little is known about the effects of extensive

artificial selection on physiological performance and metabolic demands of the

different breeds of dog (but see Bermingham et al., 2014; Careau et al., 2010;

Speakman et al., 2003).

With the highest sustained metabolic rates on record (approx. 4,400 J·kg^{-1}·day^{-1} while racing 490 km in three days at approx. -20° C; Hinchcliff et al., 1997), canids

are considered among the most elite endurance athletes in the natural world (Snow

1985; Poole & Erickson 2011; Miller *et al.* 2015). This compares to approximately

3,900 J·kg^{-1}·day^{-1} for lactating mice raising artificially large litters (14 pups) in a cold

environment (5° C; Hammond et al., 1994), 2,000 J·kg^{-1}·day^{-1} for thoroughbred horses

during heavy training (Pagan & Hintz 1986; Lewis 1995), and 1,400 J·kg^{-1}·day^{-1} for

Tour de France cyclists (Westerterp *et al.* 1986). Dogs, coyotes, wolves, and foxes

exhibit aerobic performance capacities roughly three times greater than those of

equivalently-sized terrestrial mammals (Seeherman *et al.* 1981; Weibel *et al.* 1983,

2004; Taylor, Karas & Weibel 1987a; Weibel & Hoppeler 2005). Dogs, for example,

have aerobic scopes (the ratio of maximum oxygen uptake ($\dot{V}O_{2MAX}$) to basal

metabolic rate) of 20-30, compared with aerobic scopes of about 10 for goats of equal

body mass (Weibel *et al.* 1987). To facilitate this greater oxygen capacity, dogs

possess structural and functional adaptations at each step in the pathway for oxygen,

including in the muscle mitochondria, muscle microvasculature, heart, and lungs

(reviewed in Taylor et al., 1987b). Together, the wide aerobic scopes exhibited by

canids are consistent with an ability to run for extended periods at sustained speeds

without becoming anaerobic (Okarma & Koteja 1987; Koteja 1987).

Given these physiological and morphological characteristics, both domestic and wild canids provide a unique opportunity to investigate mammalian exercise performance and energy expenditure. The expectation is that aerobic capacity provides a selective advantage for wild canids (Okarma & Koteja 1987). In the wild, the rates at which individuals acquire, transform, and expend energy (*i.e.*, their metabolic rates) are integrative measures of organism function that have fundamental consequences for survival and reproductive success (Brown *et al.* 2004; Halsey 2011). For many highly mobile species such as canids, the energetic costs associated with activity and movement form a substantial portion of daily energy expenditure (Garland 1983; Tatner & Bryant 1986; Boisclair & Leggett 1989; Karasov 1992; Gorman *et al.* 1998; Girard 2001; Weibel *et al.* 2004; Rezende *et al.* 2009; Scantlebury *et al.* 2014). In wolves and dogs, movement costs are superimposed on elevated energy demands associated with large body size (Peters 1983), endothermy (Bennett & Ruben 1979), and carnivory (Carbone *et al.* 2007, 2011), suggesting a key selective advantage for minimizing locomotor costs.

Here, we examined how selective breeding and domestication may have disrupted the optimization of these locomotor costs and altered the economy of movement in domestic dogs. This was accomplished by comparing the locomotor kinematics and energetics of three large (>20 kg) breed groups along a continuum of relative genetic and morphological proximity to gray wolves. Northern breed individuals included Siberian Huskies, Alaskan Malamutes, and Samoyeds. These "sled dogs" are among the oldest domestic dog breeds (Huson *et al.* 2010; Parker

2012; Wang *et al.* 2013) and possess the most lupine traits (*i.e.,* bear the greatest morphological and genomic resemblance to their wild progenitor, the gray wolf (Mech 1970; Parker *et al.* 2004; Udell, Dorey & Wynne 2010; Vonholdt *et al.* 2010; Skoglund *et al.* 2015)). Northern breeds have been traditionally used to assist humans with long-distance activities including arctic hunting expeditions and sledge pulling (Rennick 1987). Scent hounds, such as the Plott hounds measured in the present study, were primarily bred to aid hunters by tracking the scent of wild game (American Kennel Club 2006), an activity that requires speed but only intermediate levels of aerobic endurance relative to northern breeds. Retrievers (e.g. Golden, Labrador, Flat-coated) were also bred to assist in hunting, but typically require shorter, largely anaerobic bouts of activity to retrieve killed or injured game (American Kennel Club 2006). Because the genomic and morphological effects of dog domestication have been described (e.g. Drake et al., 2015; Freedman et al., 2014; Parker, 2012; Skoglund et al., 2015), our goal was to assess the coincident energetic consequences of human-induced selective pressures for various physical traits (e.g. limb length, body mass) and desired tasks (e.g. guarding, hunting, pulling loads). We found that working breeds of dogs most similar to wolves (i.e. northern breeds) have lower metabolic transport costs than hounds and retrievers, which have undergone divergent artificial selection trajectories from this wild canid progenitor.

Methods

Study Design

11

We quantified the overground stride mechanics, kinematics, and preferred speeds of steady-state walking, trotting, and galloping in three breed groups of domestic dogs differing in genomic relatedness to the gray wolf. These data were then paired to the gait-specific metabolic demands of level exercise for these animals measured by open-flow respirometry. Metabolic rates across each gait, total and net cost of transport, as well as the cost per stride were used to compare overall locomotor energy economy across the dog breeds. Assuming that the genetic distance from wolves approximates the relative extent of domestication (Parker 2012), we then used the breed-specific data to assess the potential effect of increased domestication on the economy of movement in dogs.

Animals

The study consisted of 23 healthy, adult dogs (2 to 11 years old) in three breed categories: northern breeds (N=9), hounds (N=7), and retrievers (N=7; Table 2.1).

All dogs were deemed healthy, active, and without any known impairments that might influence locomotion. To ensure adequate conditioning and mitigate training effects associated with the study protocol, all subjects participated in routine outdoor exercise and were physically trained for at least one month prior to and throughout data collection. Informed written consent, animal age, and health history were obtained from all dog owners, and the study protocol was approved by the UC Santa Cruz Institutional Animal Care and Use Committee.

Gait Mechanics & Kinematic Data

To determine the physiological basis of gait selection and preferred performance parameters (Perry *et al.* 1988; Nanua & Waldron 1995; Kar, Kurien Issac & Jayarajan 2003), we analyzed the natural, unrestrained locomotor gaits of each dog with repeated outdoor kinematic trials. During each trial, dogs walked, trotted, and galloped at steady-state speed along a 10 meter transect of level ground while being filmed by high-speed (Casio EX-F1, 300 fps) and high-definition (Sony HDR-CX290/B, 1080 HD, 60p) video cameras mounted perpendicular to the test course and in the dog's cranial-caudal sagittal plane.

Videos were analyzed (Corel VideoStudio ProX5, Ottawa, ON, Canada) for animal speed and basic stride mechanics (stride length, stride frequency). Given the dynamic and geometric similarity of the subjects (Alexander & Jayes 1983; Alexander 1984, 2005), dimensionless Froude numbers (speed^2/limb length · gravitational acceleration) were computed for gait transitions to compare breeds after accounting for limb length. We excluded from analysis all passes in which the dog visibly changed gait or speed mid-transect, turned its head, or otherwise deviated from a straight-line path. The preferred range of speeds for each gait was then calculated for each animal and used to ensure that subsequent metabolic treadmill trials approximated the preferred walking, trotting, and galloping speeds of the individual dog.

Previous studies report that, overall, dog sagittal-plane gait patterns on a level treadmill do not differ from those of overground locomotion (Torres *et al.* 2013),

although the stance phase is slightly longer (Fischer & Lilje 2011). We tested these findings, and closely examined gait kinematic differences across breeds, using a random subset of at least four dogs within each breed group. Anatomical landmarks on the limb joints were determined via manual palpation while flexing and extending each joint, then digitized and tracked at 300 Hz from high-speed videos (Tracker Video Analysis and Modeling Tool, http://physlets.org/tracker) to measure 24 biomechanical and kinematic parameters (Table 2.2, Table S2.1) from the subjects moving overground and on the treadmill at the same gait and speed (± 10%).

Metabolic Measurements and Energetic Costs

Because animals change gaits to achieve stability and minimize energetic costs of movement (Cavagna & Kaneko 1977; Hoyt & Taylor 1981; Bienwener 1990; Hoyt *et al.* 2006), we compared gait-specific metabolic demands across breed groups. We took simultaneous kinematic and metabolic measurements during level treadmill running for a subset of dogs according to Williams et al. (2002). For each dog, the rate of oxygen consumption ($\dot{V}O_2$, ml $O_2 \cdot kg^{-1} \cdot min^{-1}$) during rest and each gait was measured by an integrated open-flow respirometry system (TurboFOX-RM, Sable Systems International, Las Vegas, NV, USA). Following an overnight fast to ensure post-absorptive state, each animal was conditioned to rest (standing stationary or lying still in sternal recumbency), walk, trot, and gallop inside a reinforced Plexiglas metabolic chamber (1.6m x 0.5m x 1m) mounted on the surface of a variable-speed treadmill (Q65, Quinton Instrument Co, Bothell, WA, USA). The chamber was

14

equipped with a fan to facilitate rapid mixing of expired gas and prevent overheating

of exercising dogs. Each dog was weighed (Aryln 320D, East Rockaway, NY, USA)

prior to every exercise trial, and air temperatures averaged 23.4°C (range: 22 to 25°C)

within the chamber during measurements. These temperatures fell within the

thermoneutral zones of these breeds (Speakman *et al.* 2003; National Research

Council 2006). To ensure that the animals reached a physiologically stable state, each

randomized exercise trial lasted a minimum of 12 minutes; sessions that included a

pre-exercise resting metabolic rate (RMR) measurement lasted approximately 25

minutes.

Chamber air was drawn through the system with an integrated vacuum pump

at a flow rate of 230 L·min^{-1}. At this flow rate, the fractional concentration of oxygen

in the chamber remained above 0.2040 to avoid hypoxic conditions. Sub-samples of

air from the exhaust port of the chamber were drawn through a series of six columns,

alternatingly filled with desiccant (Drierite, W. A. Hammond Drierite, Xenia, OH,

USA) and CO_2 scrubber (Sodasorb, W.R. Grace & Co, Chicago, IL, USA) before

entering an oxygen analyzer. The main flow rate through the chamber, percentage of

oxygen in the expired air, humidity of the gas sample, and barometric pressure were

monitored continuously and recorded once per second on a computer using Expedata

software (Sable Systems International, Las Vegas, NV, USA). All values were

corrected to standard temperature and pressure, dry (STPD), and the entire system

was calibrated daily with ambient air (20.95% O_2 at sea level where trials occurred)

and with dry N_2 gas to test for chamber mixing and leaks according to Fedak et al.

(1981).

For each trial, average $\dot{V}O_2$ was calculated using equation 4b from Withers

(1977) and an assumed respiratory quotient of 0.82 for dogs consuming a

conventional, mixed diet (Raab, Eng & Waschler 1976; Speakman *et al.* 2003).

Physiological measurements, including energetic cost per kilogram per unit distance

(cost of transport, COT, $J \cdot kg^{-1} \cdot m^{-1}$) and cost per stride ($J \cdot kg^{-1} \cdot stride^{-1}$), were derived

from speed and stride frequency, respectively, using an energy conversion of 20.1 J

per ml O_2, assuming a negligible contribution from anaerobic glycolysis (Taylor,

Heglund & Maloiy 1982; Schmidt-Nielsen 1997). Total cost of transport (COT_{TOT})

was derived from the slope of the energy expenditure-speed relationship for each

breed; i.e. COT_{TOT} was calculated for each trial measurement by dividing mass

specific metabolic cost by the trial speed. Net cost of transport (COT_{NET}) was

calculated by subtracting the mean RMR of each individual from the energetic cost of

the trial, then dividing by trial speed. Both COT_{TOT} and COT_{NET} include any postural

costs during locomotion (the difference between mean RMR and the y-intercept in the

energy expenditure-speed relationship; Halsey, 2013; Halsey, 2016).

During the metabolic measurements on the treadmill, we recorded stride

length and stride frequency using high-speed and high-definition cameras (described

above) mounted in the sagittal plane on the right side of each dog at a distance of 1.65

meters. The timing intervals for sequential cycles of the right forelimb were averaged

from the video sequences, and the number of strides taken per second was calculated for each gait (Williams *et al.* 2002).

Statistical Analysis

Statistical analyses and figures were produced using JMP Pro12 (SAS Institute Inc., Cary, NC, USA) and R (v. 3.1.1, http://www.r-project.org/). We used principle components analysis (PCA) and linear discriminant analysis (LDA) in tandem to compare kinematic parameters across breed groups while controlling for locomotor gait. To determine the potential effect of the treadmill on kinematics, we performed paired student's t-tests (two-tailed) comparing the stride frequency and stride length for treadmill and overground locomotion within the same individual and breed group. Differences in age (years), body mass (kg), and limb length (m) between groups were determined by one-way analysis of variance (ANOVA) followed by Tukey-Kramer Honest Significant Difference (HSD) tests. We also used ANOVA with HDS to compare mass-specific $\dot{V}O_2$ and stride mechanics by gait across groups. Predicted (Heglund & Taylor 1988) and measured preferred speeds for each gait, and transitions between gaits, were compared using paired student's t-tests. We used analysis of covariance (ANCOVA) and least square linear regressions to determine the relationships between running speed and mass-specific metabolic rate, stride frequency, and stride length for each individual and breed group. For all linear models, we checked the assumptions of linearity, normality, and homoscedasticity by visual inspection of plotted residuals. To examine differences in metabolic COT

17

across breeds, we fit a three-parameter exponential decay model and determined whether 95% confidence intervals for each breed group overlapped with the estimates of the other two groups. All model combinations were fitted with best model fits based on the lowest Akaike information criteria corrected for small sample size (AICc), and study results are expressed as the mean $\pm$ s.e.m. ($\alpha = 0.05$, a priori).

Results

Gait Mechanics

Dog breed groups did not differ significantly from one another in age ($F_{2, 20} = 0.07$, $p = 0.934$), body mass ($F_{2, 20} = 3.0$, $p = 0.072$), forelimb length (i.e. withers or shoulder height above ground; $F_{2, 17} = 3.18$, $p = 0.067$), or hindlimb length (hip height above ground; $F_{2, 17}$: 2.81, $p = 0.088$, Table 2.1). However, dog breed groups differed significantly in several of the basic overground stride mechanics measured (Table S2.2). For example, there was wide variation in the range of speeds selected for each gait (walk, trot, and gallop) across breed groups (Fig. 2.1, Table S2.2). Relative to hounds, northern breeds walked, trotted, and galloped over a broader range of speeds (Fig. 2.1). Retrievers showed a contracted speed range for trotting but the largest breadth of galloping speeds (Fig. 2.1). According to the average travel speed for each gait, the three breed groups did not differ from one another while walking ($F_{2, 134} = 0.279$, $p = 0.76$), but did for faster gaits (Table S2.2). Retrievers trotted at significantly faster speeds than hounds ($t_{119} = 1.97$, $p = 0.01$) but not northern breeds ($t_{168} = 1.97$, $p = 0.13$). Furthermore, mean galloping speed was faster for retrievers

than for both hounds and northern breeds ($F_{2, 211} = 17.83$, p < 0.001, Table S2.2).

Across groups, walk-trot transition speeds ($F_{2, 20} = 0.22$, p = 0.81) and Froude

numbers ($F_{2, 18} = 1.1$, p = 0.36) did not differ across groups, indicating locomotor

similarity at slow speeds. However, at the physiologically equivalent transition from

trotting to galloping (Taylor *et al.* 1982), retrievers ran at faster speeds ($F_{2,20} = 4.19$, p

= 0.03) and Froude numbers ($F_{2,17} = 5.27$, p = 0.02) than did northern breeds or

hounds.

Hounds ($t_6 = 5.02$, p = 0.002) and retrievers ($t_6 = 2.56$, p = 0.043), but not

northern breeds ($t_8 = 1.4$, p = 0.2), trotted at speeds significantly faster than predicted

for quadrupeds of similar body mass. Hounds and retrievers also transitioned from

trot to gallop at speeds that were faster than predicted by body mass (18-26% faster, p

= 0.002-0.007 range, Fig. 2.2). Only retrievers exhibited preferred galloping speeds

faster than those predicted by Heglund and Taylor (1988) ($t_6 = 2.83$, p = 0.03).

Kinematics

After controlling for individual, gait, and speed, we found no consistent effect

of the treadmill relative to overground locomotion on sagittal plane joint flexion and

extension (Torres *et al.* 2013) and therefore assumed treadmill trials were

representative of free-ranging dog locomotion. While not significantly different (p =

0.07-0.09 range), limb lengths were generally shorter in hounds than in other breeds

(Table 2.1). To account for this, we used relative limb protraction and retraction

length values (dividing by limb length of each dog) in subsequent analyses (Table

2.2). After using PCA and LDA to condense the initial set of 24 measured kinematic

parameters down to 18 variables loaded onto 5 factors as determined by Eigenvalues

> 1, we detected group-wide differences in trotting (Wilk's $\lambda = 0.002$, $p = 0.038$), but

not walking (Wilk's $\lambda = 0.042$, $p = 0.88$) or galloping (Wilk's $\lambda = 0.002$, $p = 0.35$).

Upon closer analysis of each gait with ANOVA, we found that relative to hounds and

retrievers, northern breeds had the greatest vertical displacement while walking ($5.2 \pm$

1.4 cm, $F_{2,\ 17} = 5.0$, $p = 0.02$), and that this displacement exceeded that of their trot

(4.5 ± 0.9 cm, Table 2.2). While trotting, forelimb retraction length was greater in

hounds than in retrievers ($t_{13} = 2.1$, $p < 0.01$), and forelimb retraction angle was

greatest in hounds relative to both other groups ($F_{2,\ 18} = 10.54$, $P < 0.01$, Table 2.2).

During the gallop, northern breeds showed longer forelimb stance durations ($F_{2,\ 10} =$

17.27, $p < 0.001$) and protraction lengths ($F_{2,\ 10} = 5.94$, $p = 0.02$) than hounds and

retrievers (Table 2.2). In contrast, the duration of the forelimb galloping swing phase

was significantly longer for retrievers than for northern breeds ($t_{10} = 2.23$, $p < 0.01$,

Table 2.2).

Energetics

Because body mass differences between groups can bias mass-specific

comparisons of oxygen consumption (Packard & Boardman 1999), we first tested for

a possible effect of mass. We used ANCOVA with resting oxygen consumption as the

dependent variable, breed group as the main factor, and body mass as a covariate. The

general linear model was highly significant (GLM: $F_{5,\ 183} = 8.2$; $p < 0.0001$), but body

mass was not a significant covariate (mass: df $= 1$, F $= 2.5$; p $= 0.12$), nor was its interaction with breed group significant (breed*mass interaction: df $= 2$, F $= 2.9$, p $= 0.08$). We therefore assumed that mass-specific oxygen consumption rates appropriately account for the effect of body mass within the comparatively small mass range of the dogs in our study. We used these rates for all subsequent analyses to compare energy demand of the dogs to data from other studies typically reporting $\dot{V}O_2$ on a mass-specific level.

For all dogs, mass-specific metabolic rate increased linearly as a function of locomotor speed (Fig. 2.3), as described previously for wild and domesticated canids (e.g. Taylor et al., 1982; Weibel et al., 1983) and the majority of other terrestrial quadruped species (Taylor et al. 1982), according to

$$\dot{V}O_{2\ NORTHERN} = 7.5 + 6.16 \cdot speed \quad (r^2 = 0.87, N = 84, p < 0.001) \quad (Eqn.\ 2.1)$$

$$\dot{V}O_{2\ HOUND} = 10.46 + 8.64 \cdot speed \quad (r^2 = 0.9, N = 42, p < 0.001) \quad (Eqn.\ 2.2)$$

$$\dot{V}O_{2\ RETRIEVER} = 5.72 + 8.74 \cdot speed \quad (r^2 = 0.89, N = 48, p < 0.001) \quad (Eqn.\ 2.3)$$

where $\dot{V}O_2$ is in ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ and speed is in $m \cdot s^{-1}$. Hounds had elevated mass-specific $\dot{V}O_2$ across the range of measured trial speeds relative to both northern breeds and retrievers (Fig. 2.3). Consequently, gait-specific metabolic demands were higher for hounds while walking and trotting ($F_{2, 50} = 4.7$, p < 0.01 and $F_{2, 83} = 16.0$, p < 0.01, respectively), although galloping energetics did not differ across breeds ($F_{2, 5} = 1.1$, p $= 0.41$). Hounds also exhibited higher and longer mass-specific stride frequencies and lengths, respectively, than retrievers and northern breed dogs during treadmill locomotion.

COT_{TOT} ($J \cdot kg^{-1} \cdot m^{-1}$), which includes locomotor, postural, and maintenance

costs associated with each animal's RMR (Schmidt-Nielsen 1972, Williams 1999),

decreased with speed for all individuals within and among dog breed groups (Fig.

2.4a). Those breeds moving at faster running speeds maximized transport economy.

At comparable speeds, northern breeds exhibited lower COT_{TOT} than both hounds and

retrievers, as indicated by the significantly lower asymptote in our 3-parameter

exponential decay model (Table S2.3). Compared to COT_{TOT} of all running mammals

(including other canids) presented in Taylor et al. (1982), transport costs for northern

breeds were considerably lower than predicted by body mass (Fig. 2.5). COT_{NET},

which includes locomotor demands (including those associated with the posture

evoked during locomotion; Halsey, 2016) but not RMR, was also lowest for northern

breeds (Figs. 4b, S2.1, Table S2.3). Overall relative metabolic costs associated with

both maintenance and locomotion were lowest for northern breeds as mass-specific

resting costs were similar (approx. 6-8 ml $O_2 \cdot kg^{-1} \cdot min^{-1}$) across breed groups (Fig.

S2.1).

Faster speeds significantly reduced the mass-specific energy cost per stride

($J \cdot kg^{-1} \cdot stride^{-1}$) for hounds (cost per stride = -0.299·speed + 5.49, $r^2 = 0.14$, N = 29, p

= 0.049) but not retrievers (p = 0.112) or northern breed dogs (p = 0.7). Across all

speeds, the mean metabolic cost per stride was significantly lower for northern breeds

(3.47 ± 0.09 $J \cdot kg^{-1} \cdot stride^{-1}$) than retrievers ($3.84 \pm 0.12$ $J \cdot kg^{-1} \cdot stride^{-1}$) and hounds

(5.0 ± 0.15 $J \cdot kg^{-1} \cdot stride^{-1}$; p = 0.05 and p < 0.001, respectively; Fig. 2.4c). Indeed,

energetic demands associated with trotting in northern breeds were significantly

lower than those of walking and galloping ($F_{2, 67}$: 6.7, p = 0.002; Fig. 2.4), indicating the metabolic economy of trotting relative to both slower and faster gaits in this group. Fore and hindlimb foot contact time (t_c) were positively related to these costs per stride in hounds (cost per stride = $3.13 + 4.64 \cdot t_c$, $r^2 = 0.84$, p < 0.01; cost per stride = $3.17 + 4.5 \cdot t_c$, $r^2 = 0.89$, p < 0.01, respectively), but had no effect on retriever and northern breed dogs (p = 0.67-0.82 range).

Discussion

Although dogs in general possess a suite of adaptations for aerobic locomotion (reviewed in Taylor et al., 1987b), the between-group differences we observed in the present study reflect a physiological signature of artificial selection in the economy of running by different dog breeds. We found that that this was manifested as breed-specific differences in both overground stride mechanics and treadmill-derived movement energetics among northern breed, hound, and retriever groups. Thus, faster speeds promoted maximum economy for all dogs, but northern breeds had the lowest COT_{TOT}, COT_{NET}, and cost per stride levels relative to hounds and retrievers when trotting and galloping (Fig. 2.4).

Our hypothesis, that dog breeds more closely related to their grey wolf progenitor have relatively lower COT, was empirically supported (Figs. 2.4 and S2.1, Table S2.3). Hounds and retrievers are both relatively modern breeds compared with the ancient lineage that includes northern breed dogs (Parker *et al.* 2004; Huson *et al.* 2010; Vonholdt *et al.* 2010; Wang *et al.* 2013). Genetically the ancient breeds cluster

together closest to gray wolves, but the group is surprisingly diverse in morphology and origin. This group includes the Akita and Chow Chow of Asian origin, the Saluki and Afghan Hounds from the Middle East, the African Basenji, and the northern breeds we assessed (Parker 2012). Our study suggests that over the last ≥15,000 years of domestication, selective breeding has altered the aerobic locomotor economy of dogs, with the northern breeds retaining an economical physiological foundation that originated with gray wolves. To date, the limited existing data on the metabolic cost of running in wolves (Taylor *et al.* 1982; Weibel *et al.* 1983) does not indicate superior locomotor energy economy in wolves. However, comparisons with the current study may be misleading as a result of the adult ages of our dogs and the immature age of the wolves in the previous studies. Consequently, additional studies that measure ecologically relevant metabolic rates of adult wolves at endurance speeds are needed to determine the similarities or differences in locomotor energetics of wolves and domesticated dogs of comparable morphology and age.

To determine whether interbreed differences in energetic costs per stride were related to variation in gait patterns, we compared the Froude numbers for each breed at the walk-trot and trot-gallop transition speeds. Previous work has shown that animals of different masses but moving at the same Froude number are dynamically similar, and hence use the same gait, have comparable foot phase relationships, relative stride lengths, and duty factors, and exert similar ground reaction forces (Alexander & Jayes 1983; Alexander 1984, 2005). At the walk-trot gait transition, our results reflected those of prior studies (e.g. Jayes and Alexander, 1978; Maes et al.,

2008) where dogs began trotting at Froude numbers ≤ 0.5. However, dogs in our study began galloping at Froude numbers around 1 (mean = 0.93 ± 0.07), much lower than the predicted Froude numbers ≥ 3 reported in the previous studies. Both lower sample sizes and space constraints of the previous studies (Jayes and Alexander, 1978; Maes et al., 2008) may have contributed to these differences in Froude numbers when comparing our trials of 23 individual dogs running off-leash along an outdoor course.

When compared to the gait mechanics predictions of Heglund and Taylor (1988), we found that hounds and retrievers, but not northern breeds, trotted and transitioned from trot to gallop at speeds significantly faster than expected based on body mass (Fig. 2.2). The original study by Heglund and Taylor (1988) developed allometric equations concerning the effects of body size on stride mechanics from 16 species of wild and domestic quadrupeds ranging in mass from 30 g mice to 680 kg horses. Domestic dogs represented the only carnivore species in their analysis. It is noteworthy that in the present study, the two breed groups that differed significantly from the predicted mechanics, the hounds and retrievers, also showed significantly higher mass-specific COT and stride costs for these gaits than northern breed dogs (Fig. 2.4). In contrast, the stride mechanics of the northern breeds were as predicted. Overall, centuries of selective breeding for hunting performance in hounds and retrievers may have increased the preferred speed range for these breeds (Fig. 2.1, Table S2.2) with ensuing reduced locomotor economy (Fig. 2.4, Table S2.3).

Despite differences in basic stride mechanics across breeds, detailed kinematic analyses revealed limited distinctions between groups. Based on 24 kinematic parameters, we found larger forelimb retraction lengths and angles while trotting for hounds compared with northern breeds and retrievers (Table 2.2). This wider forelimb swing resulted in longer stride lengths and faster stride frequencies for hounds, which may have contributed to their higher COT and stride costs while trotting (Fig. 2.4). In contrast, northern breeds were the only group in which the mass-specific stride costs associated with trotting were significantly lower than those of both walking and galloping (Fig. 2.4c), resulting in relative energy economy for this intermediate-speed gait. This group also exhibited reduced vertical displacement while trotting compared to walking (Table 2.2). Such "spring dampening" while loading the Achilles tendon at speed reduces damaging vibrations and enhances forward propulsion with subsequent energy savings (Hermanson 1997; Wilson, van den Borget & McGuigan 2000; Wilson *et al.* 2001; Alexander 2001; Reilly, McElroy & Biknevicius 2007), which is consistent with our metabolic measurements (Fig. 2.3).

More generally, most terrestrial quadrupeds exhibit two unique mechanisms for reducing muscular work, and hence energy expenditure, during locomotion: pendular and mass-spring dynamics (Cavagna & Kaneko 1977; Cavagna, Heglund & Taylor 1977; Biewener 2006; Hoyt *et al.* 2006). At walking speeds, animals' exchange kinetic energy with potential energy of their center of mass (CoM) through an inverted pendulum mechanism (Cavagna *et al.* 1977; Griffin, Main & Farley

2004). Pendular energy savings persist even for loaded and incline locomotion (Gomeñuka *et al.* 2014; Pontzer 2016), although the benefits of this mechanism diminish at faster speeds (Gomeñuka *et al.* 2016). For running gaits, a spring-mass mechanism predominates, where stretched elastic structures (ligaments and tendons) store and recover mechanical energy (Cavagna *et al.* 1977, 1988; Blickhan 1989). In the present study, the economical trotting gait of northern breed dogs likely suggests an optimized spring-mass energy savings compared to other breeds. This is consistent with observations of these animals during endurance activities and races. For example, Greenland sled dogs are capable of trotting at 2.5 $m \cdot s^{-1}$ for 8-10 hours each day for 2-3 days, covering 60-80 km daily (Gerth *et al.* 2010). Similarly, wolves routinely travel in the trotting gait at the same speed (2.4 $m \cdot s^{-1}$; Mech, 1994) and can cover 76 km in 12 hours (Mech & Cluff 2011).

Foot t_c, described as the stride's stance phase duration, decreases as a power function of speed (Hoyt, Wickler & Cogger 2000) and has been shown to be inversely related to the energy expended per stride (Alexander & Ker 1990; Kram & Taylor 1990). Regardless of differences in the COT, we found no significant difference in hindlimb kinematics, including t_c, across gaits for the three dog breed groups (Table 2.2). Rather than limb kinematics *per se*, body posture and its relationship to kinematics may play a role in the COT of these groups. To examine this proximate mechanism, we digitally measured hip angle while standing (top of scapula to hock, Table S1) from lateral-view photographs of the study animals and American Kennel Club breed standards (www.akc.org/dog-breeds/), as well as gray wolves. Northern

breeds exhibited a more upright stance, with the hindlimbs positioned closer to their CoM (mean hip angle = 109.4° ± 1.1, Fig. 2.6b), nearly identical to that of gray wolves (mean hip angle = 108.8° ± 1.7, $F_{3, 31}$ = 33.7, p = 0.99, Fig. 2.6a). In contrast, the hindlimbs of both hounds and retrievers were distally grounded, farther from their CoM with significantly wider hip angles than observed in northern breeds (mean hip angle = 121.4° ± 1.7 and 122.2 ± 1.2, respectively; $F_{2, 27}$ = 38.6, p < 0.001 for both, Fig. 2.6c,d). Hounds and retrievers also held their heads in more upright positions while running, relative to the comparatively flat toplines of wolves and northern breed dogs (Fig. 2.6e-h).

Although this is a preliminary assessment, there are several mechanical advantages of the upright stance and flat topline of northern breed dogs and wolves that could impact the energetic costs of running. By aligning the joints and segments of the hindlimbs more closely with the ground reaction force vector exerted at the foot (Gray 1968), the more proximal and erect orientation of northern breed hindlimbs reduces excessive bone and muscle stress (Biewener 1989). It also provides an effective mechanical advantage for loading the tendons of the leg muscles and ligaments of the foot (Biewener 1989, 1998; Alexander & Ker 1990; Reilly *et al.* 2007), likely contributing to the relative locomotor economy observed in northern breeds. These connective tissues function like "springy struts" (Wentink 1979) or pogo sticks to temporarily store, then return, the elastic strain energy necessary to move the limb and body (reviewed in Alexander, 2002; Blickhan, 1989; Ker, 1981;

Taylor, 1994) and are especially important during trotting (Cavagna *et al.* 1977; Gregersen, Silverton & Carrier 1998).

Several studies have investigated the muscle-tendon architecture of the canid hindlimb (Shahar & Milgram 2001) and its effect on speed and power generation (Pasi & Carrier 2003; Kemp *et al.* 2005; Williams *et al.* 2008), but the role of comparative functional anatomy in promoting locomotor economy across dog breeds and canids in general remains largely unexplored. Here, we speculate that specialized tendon loading and energy recovery may provide a natural mechanism enabling wolves and other large canids to track prey over long distances (e.g. Mech et al., 2015; Sheldon, 1992). When retained through domestication, such a mechanism may help explain the exceptional physiological performance of northern breed dogs during extreme distance events such as the 1,600 km Iditarod Trail race and other endurance trials (Van Citters & Franklin 1969; Hinchcliff *et al.* 1997; Gerth *et al.* 2010; Miller *et al.* 2014).

Table 2.1: Summary of morphological characteristics for the dogs examined in this study.

Breed	Sample (N: m,f)	Mass (kg)	Age (yrs)	Forelimb length (m)	Hindlimb length (m)
Northern	9: 4,5	33.1±3.8	5.9±1.1	0.59±0.03	0.56±0.03
Hound	7: 6,1	24.2±0.9	6.0±1.2	0.49±0.02	0.5±0.02
Retriever	7: 5,2	33.2±2.3	5.4±1.2	0.6±0.04	0.61±0.05

Data are mean ± s.e.m. No characteristics differed significantly ($p < 0.05$) across breeds.

Table 2.2: Kinematic parameters of each gait for northern breed, hound, and retriever groups (N = 4 for each group). Measurement units are enclosed in parentheses.

	Walk			Trot			Gallop		
Forelimb	Northern	Hound	Retriever	Northern	Hound	Hound	Northern	Hound	Retriever
Protraction length* (m)	0.547[A]	0.484[A]	0.479[A]	0.591[A]	0.499[A]	0.579[A]	0.811[A]	0.39[B]	0.548[AB]
Protraction angle (°)	28.4[A]	24.4[A]	26.7[A]	30.7[A]	29.5[A]	27.5[A]	34.11[A]	42.7[A]	39.0[A]
Retraction length* (m)	0.305[A]	0.445[A]	0.362[A]	0.401[AB]	0.551[A]	0.322[B]	0.505[A]	0.593[A]	0.44[A]
Retraction angle (°)	15.7[A]	20.8[A]	19.5[A]	17.9[A]	25.6[B]	16.5[A]	23.57[A]	28.63[A]	21.48[A]
Stride duration (s)	0.807[A]	0.912[A]	0.799[A]	0.52[A]	0.469[A]	0.529[A]	0.413[A]	0.394[A]	0.442[A]
Swing phase duration (s)	0.309[A]	0.323[A]	0.34[A]	0.274[A]	0.246[A]	0.277[A]	0.247[A]	0.273[AB]	0.35[B]
t_c (s)	0.498[A]	0.589[A]	0.458[A]	0.247[A]	0.223[A]	0.252[A]	0.166[A]	0.121[B]	0.092[B]
Hindlimb									
Protraction length* (m)	0.34[A]	0.362[A]	0.33[A]	0.337[A]	0.287[A]	0.356[A]	0.444[A]	0.38[A]	0.37[A]
Protraction angle (°)	17.7[A]	13.9[A]	18.8[A]	16.8[A]	17.3[A]	17.3[A]	20.08[A]	20.67[A]	19.55[A]
Retraction length* (m)	0.588[A]	0.608[A]	0.474[A]	0.573[A]	0.667[A]	0.547[A]	0.729[A]	0.342[A]	0.597[A]
Retraction angle (°)	28.2[A]	23.8[A]	26.2[A]	26.7[A]	31.1[A]	26.8[A]	36.43[A]	46.07[A]	31.17[A]
Stride duration (s)	0.804[A]	0.909[A]	0.79[A]	0.533[A]	0.472[A]	0.515[A]	0.413[A]	0.379[A]	0.433[A]

Swing phase duration (s)	0.294^A	0.321^A	0.313^A	0.27^A	0.262^A	0.28^A	0.325^A	0.266^A	0.248^A
t_c (s)	0.509^A	0.588^A	0.478^A	0.263^A	0.211^A	0.235^A	0.165^A	0.113^A	0.108^A
Other									
Head angle (°)	169.3^A	160.3^A	166.5^A	165.3^A	173.4^A	165.0^A	166.22^A	157.3^A	166.34^A
Vertical displacement (cm)	5.23^A	1.71^B	2.71^{AB}	4.51^A	3.62^A	3.96^A	5.6^A	7.5^{AB}	11.66^B

t_c, contact time, representing stance phase duration.
Intergroup means not connected by a common letter differ statistically ($p<0.05$).
* indicates relative linear measurement (normalized by fore or hindlimb length of the individual dog) for direct comparison.
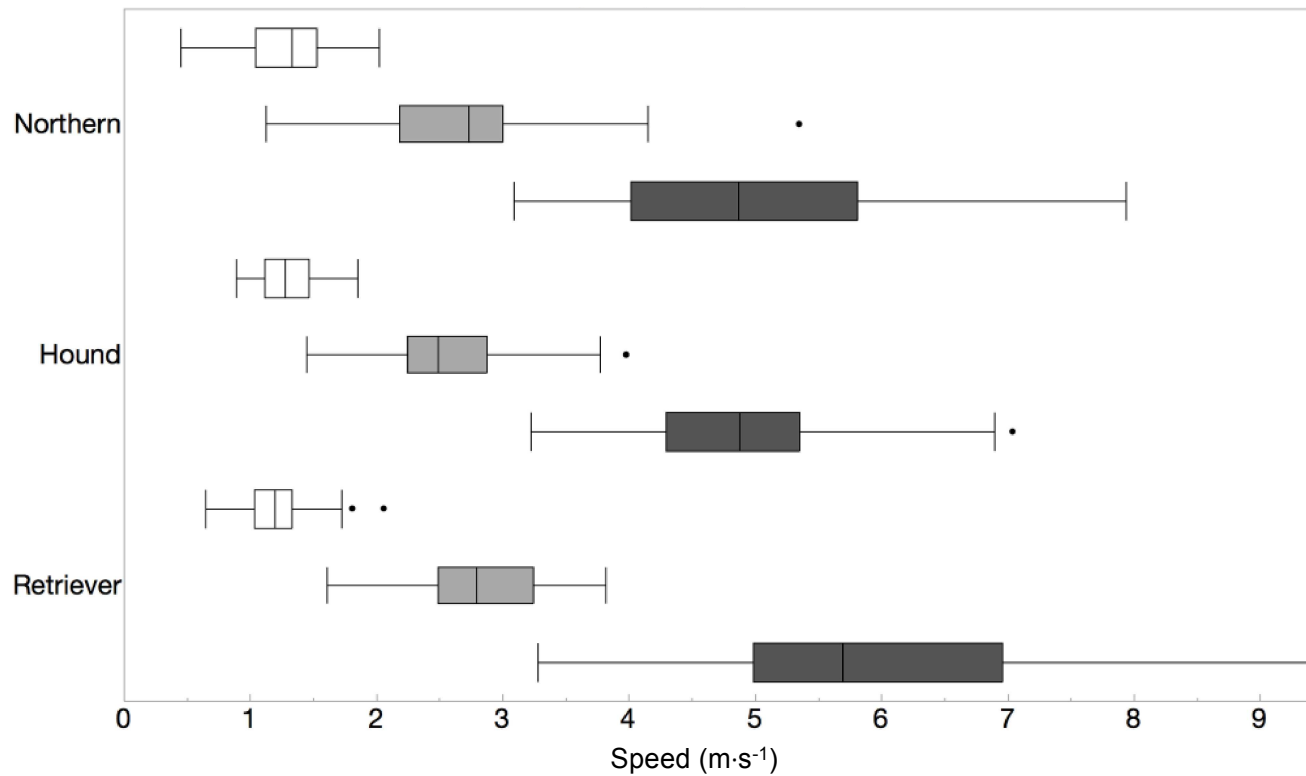
Figure 2.1: **Variation in the range of speeds (m·s^{-1}) selected for walking, trotting, and galloping by northern breed, hounds, and retriever dogs.** Box-and-whisker plots depict group-wide speed ranges (walking, white; trotting, gray; galloping, black), with the median denoted as the vertical line within each gait range quartile box. Outliers are depicted as individual points beyond the associated quartiles.
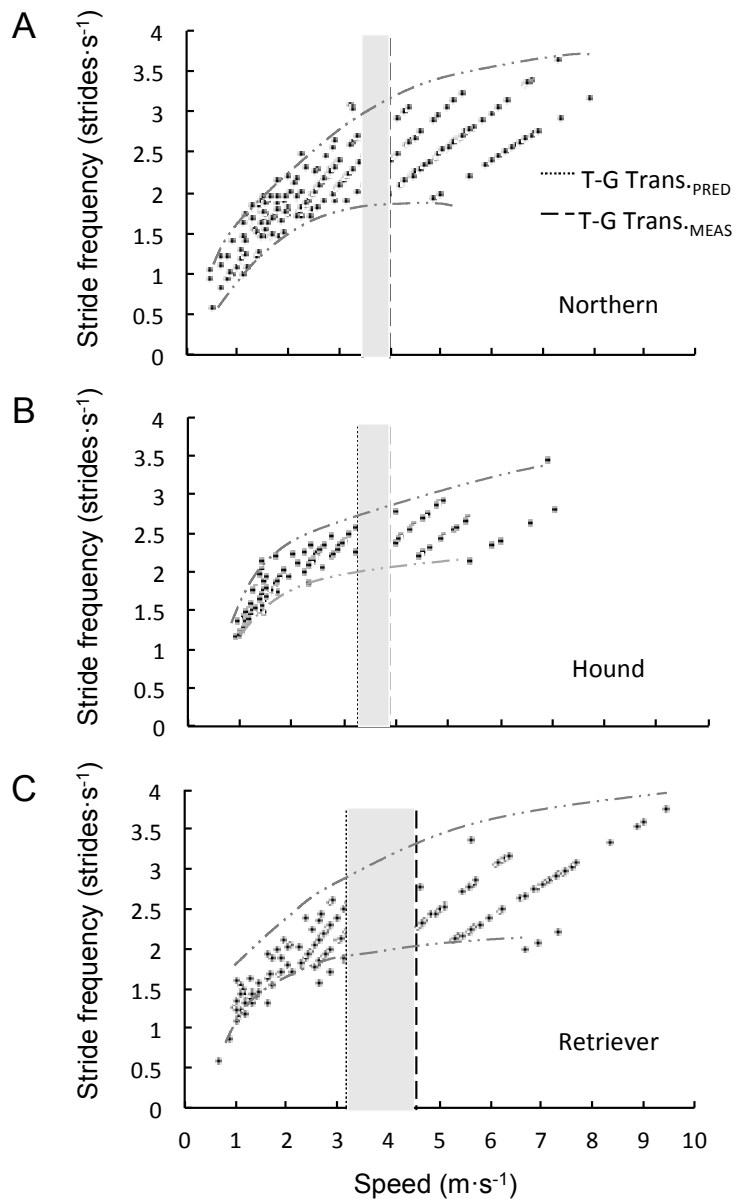
Figure 2.2: Comparison of predicted and measured physiologically equivalent trot-gallop transition speeds. (A) northern breed, (B) hound, and (C) retriever dogs. The figure shows stride frequency in relation to locomotor speed while moving on a level outdoor transect. Each data point is a single measurement for a test run by an individual dog. Dash-dot lines represent the minimum and maximum range of the data across speeds. The grey box denotes the difference between measured (dashed vertical line) and predicted (dotted vertical line) (Heglund & Taylor 1988) trot-gallop transition speeds for each breed. Pseudo-linearity of data within each group is caused by limited variation of speed-stride frequency measurements resulting from the 10 m outdoor transect length used during data collection.
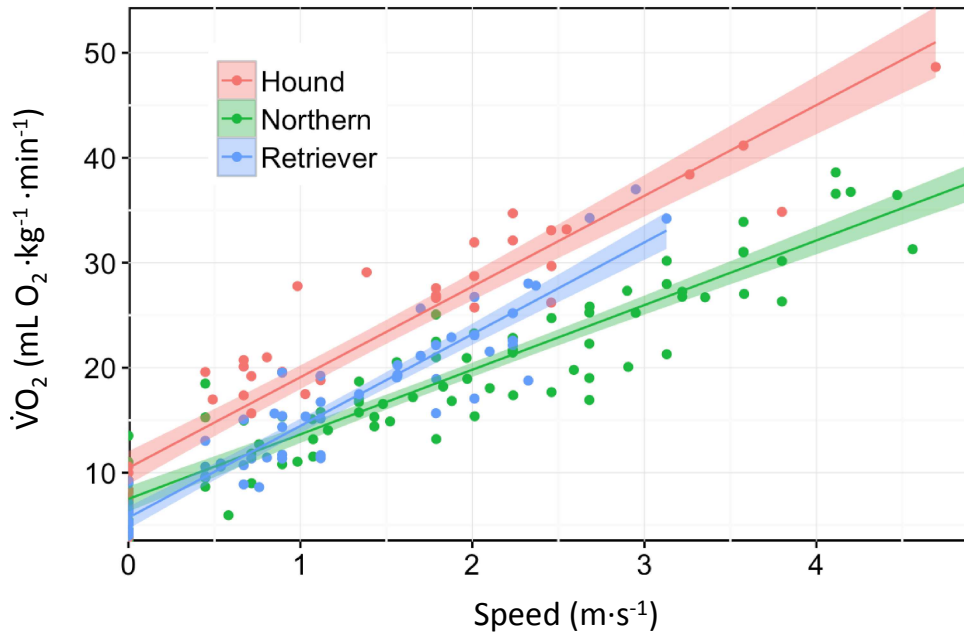
Figure 2.3: Mass-specific oxygen consumption plotted as a function of locomotor speed for northern breed, hound and retriever dogs. Each data point is a single $\dot{V}O_2$ trial measurement from a dog moving on the level treadmill at a given speed. Trials were repeated across the full range of speeds for each individual, as determined by prior outdoor running tests. The slopes of the regression lines are net cost of transport (COT_{NET}) for each breed and are presented in Eqns. 2.1-2.3.
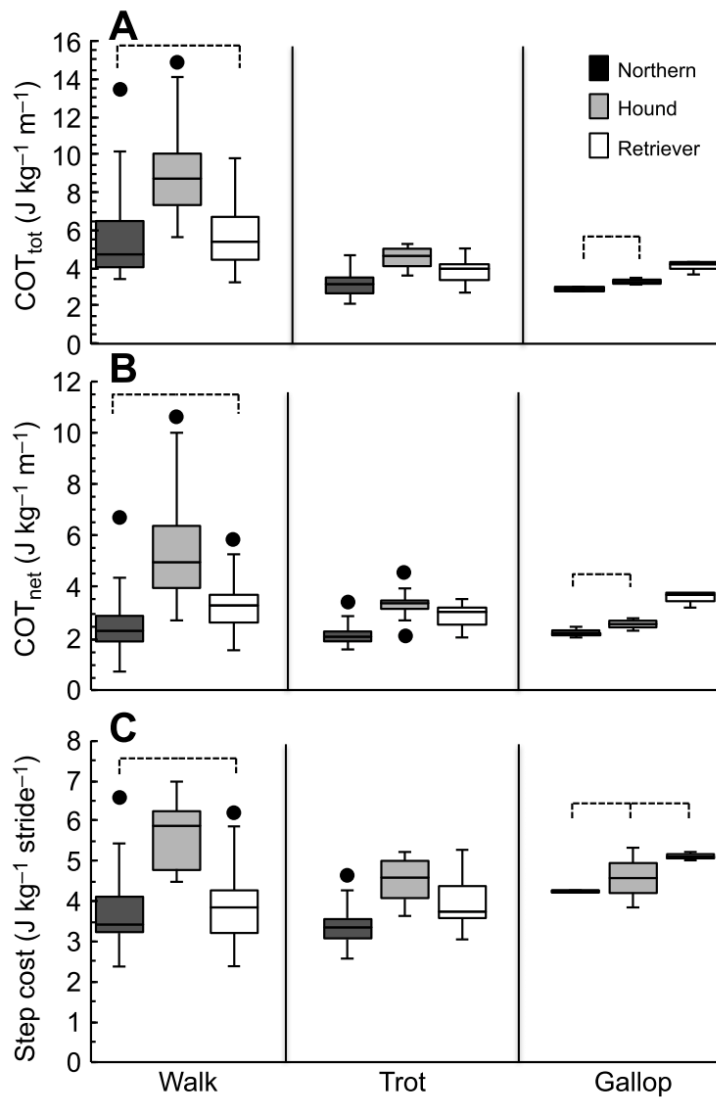
Figure 2.4: Mass-specific energetic costs associated with the cost of transport and cost per stride. (A) Total cost of transport (COT_{TOT}), (B) COT_{NET} and (C) cost per stride for running dogs. Three locomotor gaits for northern breeds, hounds, and retrievers are compared. Boxes not connected by a dashed line differ significantly (p < 0.05). COT_{TOT} was lowest while galloping for all groups, and northern breeds had significantly lower COT_{NET} and step costs than hounds and retrievers, particularly while trotting.
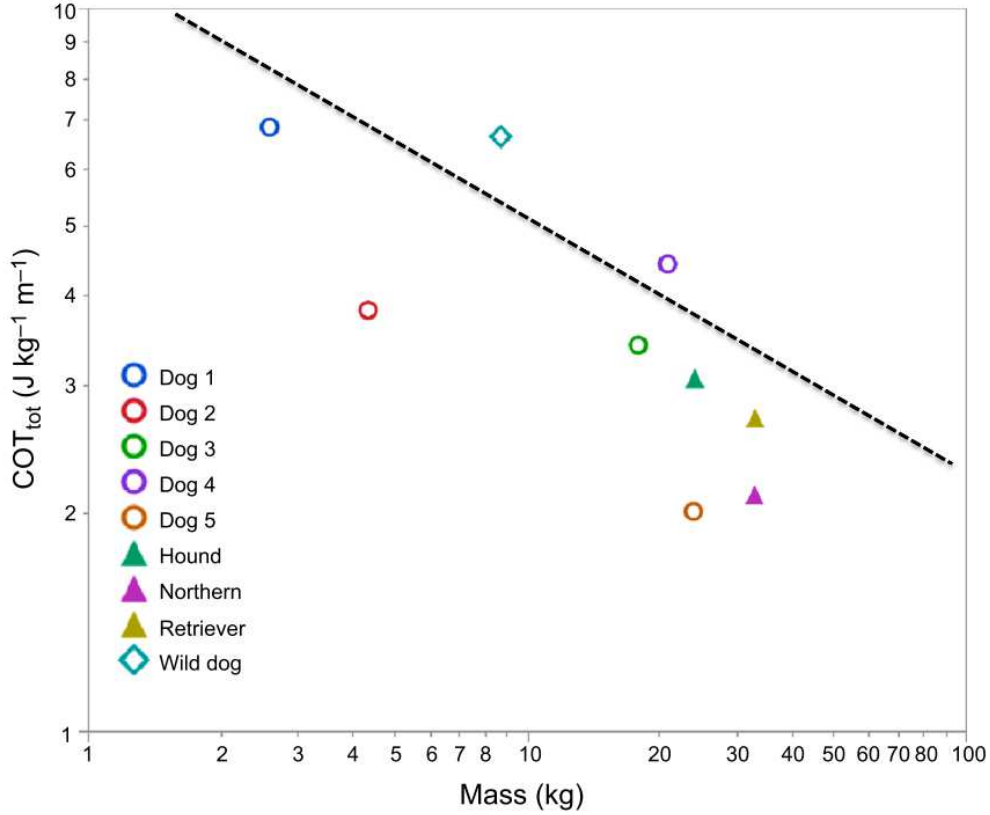
Figure 2.5: COT$_{TOT}$ for various canids in relation to the allometric regression of Taylor et al. (1982) for running mammals: COT$_{TOT}$ = 10.7×mass$^{-0.32}$ Filled triangles are data from the present study; open symbols represent data from dogs (breeds not specified) and African wild dogs running on a level treadmill as presented in Taylor et al. (1982). All dogs measured in the present study had lower transport costs than predicted by body mass, and this was particularly true for the northern breed dogs.
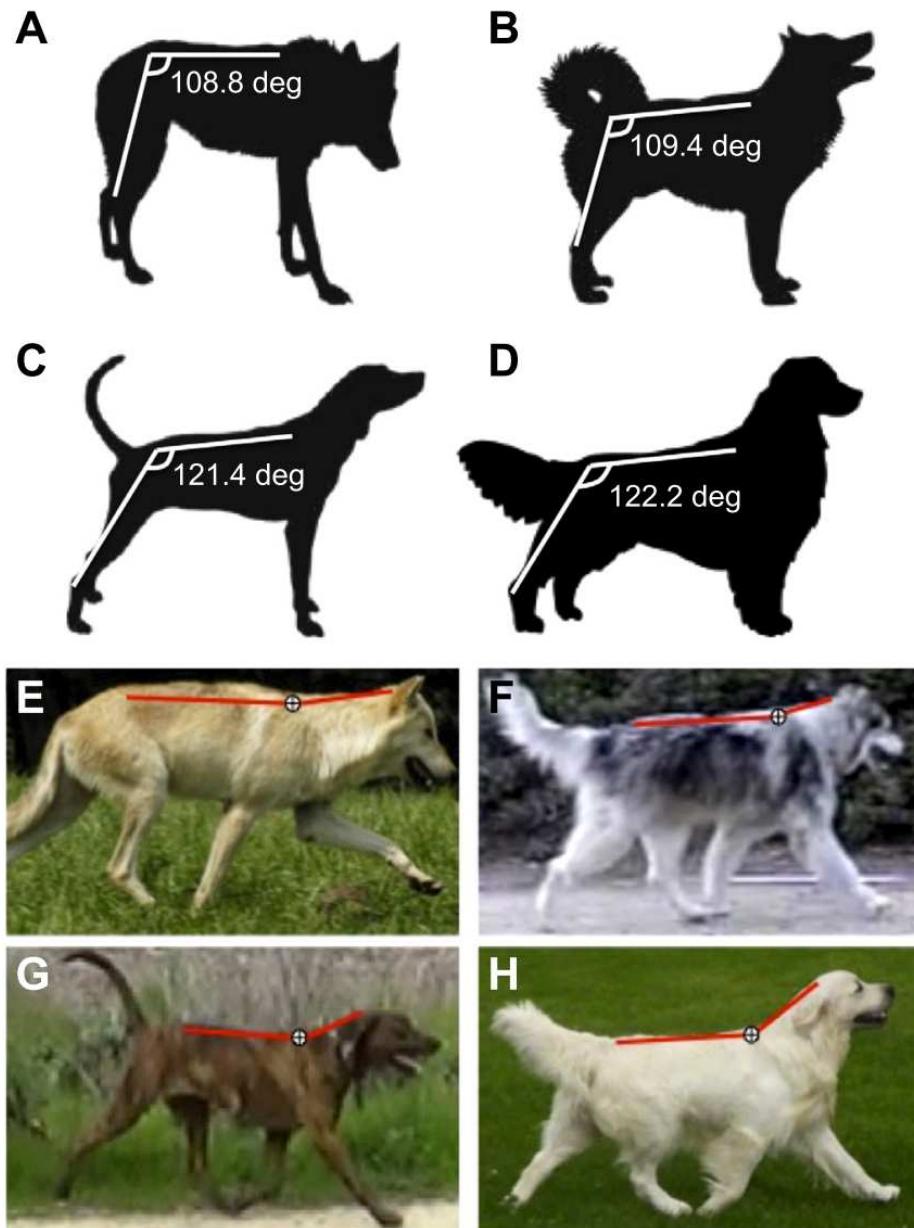
Figure 2.6: Comparative hip and topline angles of gray wolves and study dogs.
(A, E) Gray wolves (N = 5), (B, F) northern breed dogs represented by an Alaskan malamute (N = 15), (C, G), hounds (N = 5) and (D, H) retrievers (N = 10). Hip angles (A-D) were approximated from the top of scapula to the hip's iliac crest to the hindlimb hock. Canid outlines from www.clipartof.com. Topline angles (E-H) are approximated as the obtuse angle from the flat of the back to the back of the head, with hounds and retrievers running with their heads in more upright positions than observed in wolves or northern breed dogs.

Table S2.1: Kinematic parameter definitions. Measurement units are enclosed in parentheses.

Protraction length* (m)	The paw's maximum forward excursion distance, measured from the ground directly beneath the top of the scapula (withers)
Protraction angle (deg)	The angle from the paw at maximum forward excursion to the ground directly beneath the withers
Retraction length* (m)	The paw's maximum backward excursion distance, measured from the ground directly beneath the hip
Retraction angle (deg)	The angle from the paw at maximum backward excursion to the ground directly beneath the hip
Stride duration (s)	The length of time between two consecutive touchdowns of the same limb
Swing phase duration (s)	The length of time between the limb lifting off and touching down again
t_c (s)	The length of time that the limb is in contact with the ground
Head angle (deg)	The obtuse angle of the dog's head relative to its back topline (hip to withers)
Hip angle (deg)	The obtuse angle from dog's withers to the hip's iliac crest to the hindlimb hock
Vertical displacement (cm)	The maximum vertical distance covered by the dog's back, as measured from the withers

* indicates linear measurement normalized by fore or hindlimb length of individual dog for direct comparison
 t_c , contact time, representing stance phase duration

Table S2.2: Overground stride mechanics for all breeds examined across three distinct gaits.

	Walk			Trot			Gallop		
	Northern	Hound	Retriever	Northern	Hound	Retriever	Northern	Hound	Retriever
Speed (m·s^{-1})	1.27 (0.04)^A	1.28 (0.05)^A	1.23 (0.05)^A	2.7 (0.06)^{AB}	2.51 (0.09)^B	2.8 (0.07)^A	4.96 (0.11)^A	4.9 (0.2)^A	5.94 (0.14)^B
Stride frequency (strides·s^{-1})	1.5 (0.04)^{AB}	1.57 (0.05)^A	1.38 (0.05)^B	2.1 (0.03)^{AB}	2.2 (0.04)^A	2.07 (0.03)^B	2.61 (0.03)^A	2.6 (0.06)^A	2.64 (0.04)^A
Stride length (m)	0.84 (0.02)^{AB}	0.82 (0.02)^B	0.9 (0.02)^A	1.26 (0.02)^A	1.13 (0.03)^B	1.36 (0.02)^C	1.91 (0.04)^A	1.91 (0.1)^A	2.26 (0.04)^B

Data are mean (± s.e.m.)

Intergroup means not connected by a common letter differ statistically (p<0.05).

Table S2.3: Estimates and 95% confidence intervals for 3-parameter exponential decay models of dog breed mass-specific total (COT$_{TOT}$) and locomotor (COT$_{NET}$) costs of transport (J·kg^{-1}·m^{-1}) as a function of animal speed. The asymptote of each model reflects the minimum transport cost (COT$_{MIN}$) for each breed group.

		Northern		Hound		Retriever	
		COT$_{TOT}$	COT$_{NET}$	COT$_{TOT}$	COT$_{NET}$	COT$_{TOT}$	COT$_{NET}$
	Lower 95%	2.69	1.97	3.57	2.8	3.38	2.75
Asymptote	Estimate	3.01^A	2.1^A	4.17^B	3.35^B	3.81^B	2.96^B
	Upper 95%	3.34	2.23	4.76	3.91	4.23	3.17
	Lower 95%	10.51	-4.05e8	13.67	-8.67	4.5	-3214.8
Scale	Estimate	20.36^A	4.3e6^A	22.14^A	36.3^A	16.46^A	389.1^A
	Upper 95%	30.21	4.13e8	30.61	81.19	28.43	3993.1
	Lower 95%	-3.63	-244.7	-1.43	-6.53	-4.49	-33.11
Decay Rate	Estimate	-2.71^A	-31.94^A	-0.84^B	-4.16^A	-3.06^A	-12.6^A
	Upper 95%	-1.78	180.8	-0.25	-1.8	-1.63	7.92
AIC$_c$		217.2	119.2	85.6	97.7	125.5	96.8
R^2		0.69	0.58	0.90	0.62	0.65	0.24

Intergroup means that are not connected by a common letter differ statistically ($p < 0.05$).
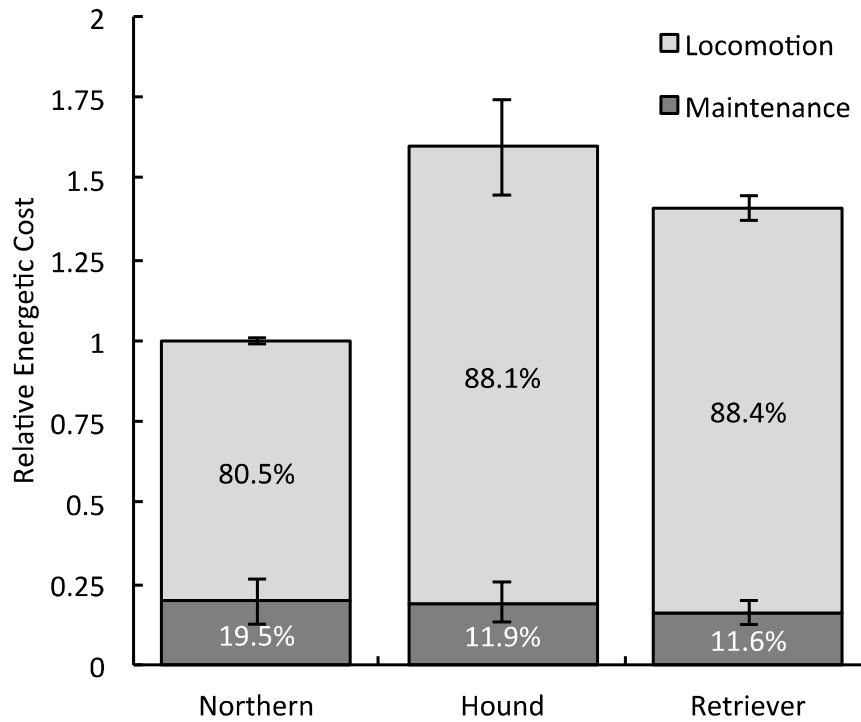
Figure S2.1: Relative mass-specific energetic demands (mean ± s.e.m. error bars) associated with locomotion (scaled from $COT_{NET,}$ $J·kg^{-1}·m^{-1}$) and maintenance costs (scaled from RMR, ml $O_2·kg^{-1}·min^{-1}$) for northern breed (n = 9), hound (n = 7), and retriever (n = 7) dogs. Overall relative metabolic costs associated with both maintenance and locomotion were lowest for northern breeds as mass-specific resting costs were similar (approx. 6-8 ml $O_2·kg^{-1}·min^{-1}$) across breed groups.

CHAPTER 3

Energetics and evasion dynamics of large predators and prey: pumas *vs.* hounds

Abstract

Quantification of fine-scale movement, performance, and energetics of large carnivores and their prey is critical for understanding the physiological underpinnings of trophic interactions. This is particularly challenging for wide-ranging terrestrial canid and felid predators, which can each affect ecosystem structure but through distinct hunting modes. To compare free-ranging pursuit and escape performance from group-hunting and solitary predators in unprecedented detail, we calibrated and deployed accelerometer-GPS collars during predator-prey chase sequences of hound packs (avg. mass = 26 kg) pursuing simultaneously instrumented pumas (avg. mass = 60 kg). We then reconstructed chase paths, speed and maneuvering profiles, and energy demands for hounds and pumas to examine physiological constraints associated with cursorial and cryptic hunting modes, respectively. Interaction dynamics revealed how pumas successfully utilized terrain (e.g., fleeing up steep, wooded hillsides) as well as evasive maneuvers (e.g., jumping into trees, running in a figure-8 pattern) to increase their escape distance from the overall faster hounds (avg.

2.3× faster). These adaptive strategies were essential to evasion in light of the mean 1.6x higher mass-specific energetic costs of the chase for pumas compared to hounds (mean: 0.76 vs. 1.29 kJ·kg^{-1}·min^{-1}, respectively). On average, escapes were exceptionally costly for pumas, requiring exercise at $\geq$ 90% of predicted $\dot{V}O_{2MAX}$ and consuming as much energy per minute as approximately 5 minutes of active hunting. These results demonstrate the marked investment of energy for evasion by a large carnivore and the advantage of dynamic maneuvers to aid in reducing total chase time.

Introduction

During a predation event, an animal's ability to rapidly adjust its speed (Howland 1974; Domenici 2001), acceleration (Combes *et al.* 2012; Wilson *et al.* 2013c), and turn capacity (Howland 1974; Maresh *et al.* 2004; Wilson *et al.* 2013b) become critical for survival. Despite its relative brevity, the attack phase of the hunt may be the most energetically expensive stage of prey acquisition, particularly for ambush predators (Williams *et al.* 2014). Given the two-dimensional confines of the terrestrial environment, both predators and prey have restricted behavioral options during this important phase and are primarily left with modulating their speed (Elliott, Cowan & Holling 1977) and/or maneuverability (Howland 1974) in order to hunt successfully or survive, respectively (reviewed in Wilson et al., 2015). Furthermore, these constraints may result in an "arms race" evolutionary escalation of matched, specialized morphologies and behavioral strategies that promote capture ability or

evasion capacity in predator-prey species pairs that have co-evolved (Brodie &

Brodie 1999; Cortez 2011), though the strength of selective forces acting on predators

vs. prey may differ (i.e. the "life-dinner principle", Dawkins and Krebs, 1979).

Similarly, hunting modes in sympatric large carnivores have also evolved and

diversified, with members of the families *Felidae* and *Canidae* exhibiting nearly

opposite prey detection and capture techniques characterized by cryptic ambushing or

cursorial pursuit, respectively (Table 1). Large canids such as gray wolves (*Canis

lupus*), often hunt cooperatively in packs (Mech 1970; Mech *et al.* 2015a) and rely on

endurance pursuit (Snow 1985; Poole & Erickson 2011), rather than speed or agility,

to test and ultimately outperform more vulnerable prey (Peterson & Ciucci 2003;

Mech *et al.* 2015a). In contrast, most large felids such as pumas (*Puma concolor*)

exhibit an opportunistic cryptic hunting mode (i.e. less selective, Husseman et al.,

2003; Wilmers et al., 2007; Kunkel et al., 1999; Okarma et al., 1997, but see Karanth

and Sunquist, 1995; Krumm et al., 2010) by which they stealthily ambush and

overpower prey (Young 1946; Hornocker 1970; Seidensticker *et al.* 1973; Koehler &

Hornocker 1991; Ruth & Murphy 2009a) through matching pounce force to prey size

(Williams *et al.* 2014). Pumas are primarily nocturnal and solitary hunters, although

females will typically raise and accompany cubs for 15-21 months after birth

(Hornocker & Negri 2009). Such divergence in locomotion, sociality, prey selectivity,

and even preferred terrain while hunting reduces exploitative and interspecific

competition through spatiotemporal niche partitioning (Husseman *et al.* 2003;

Elbroch *et al.* 2015) and has cascading, ecosystem-wide effects (Donadio and

Buskirk, 2006; Linnell and Strand, 2000; Rosenzweig, 1966). Less is known, however, of how the fine-scale movement, performance, and metabolic demands associated with these distinct hunting modes interact to affect direct felid-canid conflict or predation success.

The impacts of locomotor performance and energetics in altering chase outcomes has long been recognized, with the majority of our understanding of these interactions coming from studies of animals maneuvering in aerial (Warrick 1998; Hedenström & Rosén 2001; Combes *et al.* 2012) or aquatic (Domenici & Blake 1997; Domenici 2001; Breed *et al.* 2017; Wright *et al.* 2017) environments. Considerably less attention has been given to describing these complex dynamics in terrestrial species, particularly large carnivores and their prey (Wilmers *et al.* 2015). This is likely because our ability to describe such interactions is substantially impaired by the wide-ranging, often cryptic behaviors of these large mammals (Gese 2001; Thompson 2004; Williams *et al.* 2014; Wang *et al.* 2015b). Recently, however, advancements and miniaturization of biologging sensor technology now enable scientists to concurrently measure previously unavailable metrics including the fine-scale behavior, physiological performance, and energetics of wild animals (Kays *et al.* 2015; Wilmers *et al.* 2015). In addition, these novel tools have the capacity to quantify chase dynamics and identify features of the landscape and the animals themselves that determine whether or not prey evade capture (Wilson *et al.* 2013b).

Animal-borne accelerometers, for example, permit quantification of distinct behaviors by type, time, frequency, and intensity, thereby enabling researchers to

measure activity budgets, rare behavioral events (such as prey capture), and energy expenditure of animals in situ (reviewed in Brown et al., 2013). The derivation of an animal's overall dynamic body acceleration (ODBA), a well-supported proxy for metabolic rate (Wilson *et al.* 2006; Halsey *et al.* 2009; Gleiss, Wilson & Shepard 2011; Qasem *et al.* 2012; Brown *et al.* 2013), involves summing smoothed absolute acceleration values from each logger axis after subtracting static acceleration associated with gravity and logger position (Wilson *et al.* 2006; Gleiss *et al.* 2011). The dynamic component of body acceleration has been found to be strongly correlated with nearly instantaneous energy expenditure due to the relationship between muscle contraction and ODBA for a known body mass (Wilson *et al.* 2006; Green *et al.* 2009; Gleiss *et al.* 2011; Gómez Laich *et al.* 2011). Significant linear relationships between ODBA and speed and oxygen consumption ($\dot{V}O_2$) measured in captive animals (Halsey *et al.* 2009; Halsey, Shepard & Wilson 2011; Bidder, Qasem & Wilson 2012a; Bidder *et al.* 2012b; Qasem *et al.* 2012) permit accelerometers to quantify stepping costs (Williams *et al.* 2004, 2014) and total energy expenditure (Williams *et al.* 2004; Wilson *et al.* 2006; Wilson, Shepard & Liebsch 2008; Green *et al.* 2009; Halsey *et al.* 2009) in free-ranging conspecifics. This captive-to-wild sensor calibration approach is essential for creating species-specific behavioral-energetic signature libraries that correlate routine activities (e.g., resting, walking, and galloping) to their associated energetic costs (Halsey *et al.* 2009; Brown *et al.* 2013; Williams *et al.* 2014; Wilmers *et al.* 2015).

Here, using simultaneously instrumented pumas and hounds (*Canis lupus familiaris*), we examined the performance and energetic tradeoffs of cryptic *vs.* cursorial hunting modes in real time. Packs of trained hounds pursued solitary pumas in need of recapture for a separate monitoring study and afforded a comprehensive look at hound group hunting cohesion and its effect on puma escape tactics in rugged terrain. While we recognize that though dogs can adversely affect free-ranging carnivore behavior (e.g., Vanak et al., 2013; Wierzbowska et al., 2016), hounds chasing pumas may not be a common occurrence in the wild. We suggest, however, that the stereotyped behavioral flight response of pumas to dogs may be representative of direct interspecific interactions between wolf packs and solitary pumas in landscapes where these predators coexist. Hound-assisted puma recaptures also enabled us to record the maximal or near-maximal performance capacity of a wild felid predator, shedding light on hunting adaptations for, and limits to, managing speed, maneuverability, and energy demand during prey capture.

Given their local adaptation and stalk-and-pounce hunting mode, we predicted that pumas would exhibit greater acceleration, top speed, and maneuverability in rugged terrain relative to hounds, but could only sustain this peak performance over a short distance and duration (i.e. more intermittent locomotion). Furthermore, we predicted that the cursorial hounds would compensate for their inferior peak performance by coursing continually over long distances at slower speeds with greater energetic efficiency relative to pumas, provoking the puma to ultimately escape into a tree to evade capture. Because of the scarcity of studies investigating

detailed chase performance parameters and their associated metabolic costs in terrestrial mammals, our goal was to determine how terrain and differences in morphology, physiology, and behavioral strategies among large felids and canids affect chase dynamics and outcomes.

Methods

Collar & energetic calibrations

We used a laboratory-to-field approach in which the locomotor biomechanics and energetics of scent hounds (n = 7, 24.2 ± 0.9 kg) and captive pumas (n = 3, 65.7 ± 4.4 kg) instrumented with accelerometer-GPS collars were measured in an enclosure and laboratory environment prior to deployment on free-ranging conspecifics in the wild (Bryce and Williams, in review; Wang et al., 2015a; Williams et al., 2014; Wilmers et al., 2015). Hounds wore a 16 Hz accelerometer (TDR10-X, Wildlife Computers, Redmond, WA, USA) affixed to a GPS collar (Astro, Garmin Ltd, Switzerland) capable of taking a GPS satellite fix every 3 seconds (total collar mass = 328 g) and pumas wore an integrated accelerometer-GPS collar (GPS Plus, Vectronics Aerospace, Germany; total collar mass = 480g) that sampled acceleration continuously at 32Hz and took GPS fixes every 6-8 seconds in the field during hound-assisted puma recaptures. For both types, the tri-axial accelerometer was mounted such that the x-, y-, and z- axes were parallel to the transverse, anterior-posterior, and the dorsal-ventral planes of the animal, respectively. For collar calibration, captive pumas (Williams *et al.* 2014; Wang *et al.* 2015b) and hounds

(Bryce & Williams 2017) were trained to rest and move across a range of natural speeds (rest to 2 m·s^{-1} and 4.7 m·s^{-1}, respectively) while on a treadmill enclosed by a metabolic chamber. Collar-derived accelerometer signatures were then correlated to gait-specific locomotor costs by simultaneously measuring oxygen consumption ($\dot{V}O_2$) and overall dynamic body acceleration (ODBA; Qasem et al., 2012; Wilson et al., 2006) of the animals during steady- state resting and treadmill running (Williams *et al.* 2014; Bryce & Williams 2017). Because both speed and metabolic rate are linked to the dynamic component of an animal's body acceleration (Gleiss *et al.* 2011; Bidder *et al.* 2012a; b; Qasem *et al.* 2012), we used ODBA to translate sensor output from the collars into the speed, maneuvers, and energetics of free-ranging individuals.

Fieldwork

An estimated population of 50-100 pumas resides in our 1,700 km^2 study area in the Santa Cruz Mountains of California (37° 10.00' N, 122° 3.00' W). The climate is Mediterranean, with precipitation concentrated between November and April. Elevation ranges from sea level to 1155m, and rugged, forested canyons characterize much of the preferred puma habitat. Our study area encompasses a diverse landscape ranging from dense, urban development to large tracts of intact and relatively undisturbed native vegetation primarily comprised of redwood and Douglas fir, oak woodland, or coastal scrub communities. It is bisected by a large freeway and further transected by numerous smaller arterial (>35 mph), neighborhood (<35 mph), and

unpaved roads providing access to rural houses and developments. As a result, pumas

and native mesopredators (i.e. coyotes, foxes, and bobcats) in the region exhibit

spatial and temporal partitioning of activities that vary with human use (Wilmers *et

al.* 2013; Smith, Wang & Wilmers 2015b, 2016; Wang, Allen & Wilmers 2015a).

Previous work validated the use of GPS-accelerometer collars for describing

spatiotemporally explicit puma energetics (Williams *et al.* 2014) and behaviors

(Wang *et al.* 2015b) in the field. Here, we separately recaptured two adult male

pumas (59.7 ± 0.7 kg) in autumn 2015 using packs of 5 and 4 hounds (n = 8, 24.3 ±

0.8 kg; Wilmers et al., 2013), respectively. We took advantage of this routine capture

technique by collecting simultaneous sensor measurements and video recordings

(Sony HDR-CX290/B, 1080 HD, 60p) to quantify the detailed chase-escape dynamics

and associated energetic costs for hounds and pumas. In the field, we filmed the

hound collar being manually shaken prior to and immediately following deployment

for subsequent accelerometer and GPS clock synchronization to GMT. Similarly, we

filmed the screen (including the clock) of the handheld UHF terminal (Vectronic

Aerospace, Germany) while uploading the rapid GPS fix schedule in order to later

synchronize the exact time of the puma collar schedule upload to the hound collar

clock.

Puma chases occurred during daylight hours between 09:00 and 15:00 local

time, a period that typically corresponds with inactivity for these nocturnal hunters

(Fig. S3.1). Four total chases (2 per puma) were recorded because both pumas

escaped into trees that precluded darting after the first chase. All hounds were

released simultaneously for each recapture, and though only one hound in each chase wore the combined accelerometer-GPS collar, all hounds wore identical GPS tracking collars to enable an analysis of pack hunting dynamics. After escaping to a tree suitable for darting, pumas were tranquilized with Telazol at a concentration of 100 mg/mL, measured, and re-collared while we collected the previous collar for chase reconstruction and analysis. The Animal Care and Use Committee at UC Santa Cruz approved all animal-handling procedures (IACUC Protocol #Wilmc1101).

Analyses

From each chase, we quantified speed, maneuvering, energy demand, and the impact of landscape features for each instrumented animal. Instantaneous energetics and cost of transport (COT, the energy expended per meter) of pumas and hounds were determined by correlating ODBA, smoothed over a 2 second running mean (Wilson *et al.* 2006; Shepard *et al.* 2008a), to laboratory-derived rates of oxygen consumption. We then used Eqn. 5 from Williams et al. (2014) to compare the COT of 60 kg pumas during typical 2-hour pre-kill active hunting activity (i.e. searching and stalking) to that of the brief, high intensity escape bouts during hound-assisted recapture. To assess the extent of anaerobic exercise for each species, we compared accelerometer-derived estimates of $\dot{V}O_2$ during chases to published values of $\dot{V}O_{2MAX}$ for lions (approx. 52 ml $O_2 \cdot kg^{-1} \cdot min^{-1}$; Taylor et al., 1980; Williams et al., 2014) and dogs (approx. 160 ml $O_2 \cdot kg^{-1} \cdot min^{-1}$, Seeherman et al., 1981; Weibel et al., 1983) of comparable mass.

Overground pursuit and escape speeds were quantified by GPS-derived means for all animals, with accelerometer-derived speeds also computed for both pumas and focal hounds instrumented with combined sensors. The proportion of time spent not moving within each chase was calculated for each species based on the number 2-second windows where ODBA < 0.5 g. We downsampled all hound GPS data to fixes taken every 6s to account for differences in GPS sample rate during chases and permit direct comparisons of hound and puma spatial datasets. The precise start and end of pursuits and escapes for hounds and pumas, respectively, were determined by post-hoc comparison of GMT-synchronized video recordings obtained in the field and from each collar's raw accelerometer output. The beginning of each escape was readily apparent from puma accelerometer records, as each animal had been resting prior to hound release. Tag synchronization and data visualization was performed in Igor Pro (Wavemetrics, Lake Oswego, OR, USA). Statistical analyses and figures were produced using JMP Pro12 (SAS Institute Inc., Cary, NC, USA), program R (v. 3.1.1; R Core Team 2014), and Matlab (Mathworks Inc, Natick, MA, USA). Study results are expressed as the mean ± s.e.m. ($\alpha = 0.05$, a priori).

Results

Captive Calibrations

For both hounds and pumas, mass-specific metabolic rate increased linearly as a function of ODBA as described previously for a variety of other terrestrial

quadruped species (e.g., Brown et al., 2013; Halsey et al., 2009; Wilmers et al., 2015), according to

$$\dot{V}O_{2\ HOUND} = 22.87 \cdot ODBA + 6.39; \ (r^2 = 0.86, \ n = 83, \ p < 0.001), \quad \text{(Eqn. 3.1)}$$

$$\dot{V}O_{2\ PUMA} = 58.42 \cdot ODBA + 3.52; \ (r^2 = 0.97, \ n = 9, \ p < 0.001), \quad \text{(Eqn. 3.2)}$$

respectively, where $\dot{V}O_2$ is in ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ and ODBA is in g. Similarly, speed was strongly predicted from ODBA (Bidder *et al.* 2012a; b) for both species according to

$$Speed_{HOUND} = 2.56 \cdot ODBA - 0.32; \ (n = 83, \ p < 0.001), \quad \text{(Eqn. 3.3)}$$

$$Speed_{PUMA} = 5.32 \cdot ODBA - 0.42; \ (n = 9, \ p < 0.001) \quad \text{(Eqn. 3.4)}$$

where speed is in $m \cdot s^{-1}$ and ODBA is in g. Equations 2 and 4, as well as additional puma collar calibration data, are available from Williams et al. (2014) and Wang et al. (2015a).

Chase reconstructions

The duration, distance, average speed, elevation change, and number of hounds involved in each recapture are summarized for hounds and pumas in Table 3.2. Individual chase tracks and parameters (Fig. 3.1, S3.2-S3.4) are also presented as Google Earth Pro (earth.google.com) visualizations generated from synchronized puma and hound collar data (Videos S3.1-4). In general, mean chase distance was three times farther for hounds (1020 ± 249 m) than pumas (335 ± 63 m, t (6) = -2.66, p = 0.037, Table 3.2) because we released hounds from a distance great enough to not startle pumas prior to release. In this way, we measured the complete and varied

escape maneuvers of the puma in response to the approaching hounds. As a result of these longer pursuit distances, hound chase duration (08:59 ± 03:05 mm:ss) was longer than the associated escape time in pumas (03:48 ± 01:16). Compared to the initial escape, each puma's second flight was shorter in both distance (247 ± 69 vs. 423 ± 60 m) and duration (01:53 ± 00:56 vs. 05:44 ± 01:12, Table 3.2). Tortuosity, defined as the total distance traveled divided by straight-line distance from start to end point of run, did not differ significantly between hounds and pumas when all individuals and chases were grouped (t (22): 1.04, p = 0.31; Table 3.3). Overground distance traveled averaged 2.3 to 2.9 times farther than straight-line distance, indicating extent of turning maneuvers while running through rugged terrain. To prolong the time until captured, pumas employed several adaptive strategies that compensated for physiological constraints and being outnumbered. Evasive maneuvers such as temporarily jumping into trees, running hairpin turns or figure-of-8 patterns, and fleeing up steep, wooded hillsides were all used repeatedly to increase escape distance and postpone being overtaken.

Overall average chase speed, as measured by chase distance divided by chase duration, was comparable between species (2.7 ± 0.8 m·s^{-1} and 2.3 ± 1.09 m·s^{-1} for hounds and pumas, respectively; t (6) = -0.31, p = 0.77, Table 3.2). However, GPS-derived average speeds from all hounds (including those not outfitted with accelerometers) and pumas suggested that, across chases, hound pursuit speed was twice that of the escaping pumas (1.7 vs. 0.74 m·s^{-1} for hounds and pumas, respectively; t (1870) = -10.4, p < 0.01; Table 3.3, Fig. 3.2), since pumas spent larger

proportions of each encounter stationary (avg. 31% and 15% stationary for pumas and hounds, respectively; t (6) = 1.37, p = 0.22). Using accelerometer-derived speed estimates (Eqn. 3.3 & 3.4) to resolve running dynamics in finer temporal resolution, we note that pumas briefly hit peak speeds in excess of 14 m·s^{-1}, more than twice the top speed of the pursuing hounds (5.2-6.3 m·s^{-1}, Table 3.3). Puma escapes were characterized by sequential high-speed evasive maneuvers interspersed with slow, low acceleration periods (Fig. 3.3). In contrast, hound pursuit speeds were more constant over the course of each (Figs. 3.1c, S3.2-S3.4c).

Immediately after release, all hounds concurrently worked to detect the nearby puma's scent and give chase. Average hound chase speed did not differ across individuals for both pursuits of puma 36M (chase 1: 2.52 ± 0.07 m·s^{-1}, $F_{4, 711}$: 0.71, p = 0.59; chase 2: 1.74 ± 0.03 m·s^{-1}, $F_{4, 1653}$: 1.95, p = 0.1), but Hound 4 was significantly slower than the three other hounds during both pursuits of puma 26M (Hound 4: 1.37± 0.06 m·s^{-1}, others: 1.71 ± 0.04 m·s^{-1}; t_{988}: -4.4, p<0.001). This was probably a result of Hound 4's age (11), over twice as old as the other hounds (average age of 5) involved in 26M's recapture. Hound group cohesion (the spacing of individual members in proximity to the group centroid) varied across chases (Fig. 3.4), likely due to interacting effects including pack composition, individual characteristics (e.g. experience, age, sex), topographic complexity, and puma scent freshness. Tighter spatial clustering observed between the 5 members of the hound pack pursuing puma 36M (Fig. 3.4a,b) than that of the 4-member pack that chased puma 26M (Fig. 3.4c,d). Across chases, the maximum path deviation of individual

hounds from one another averaged 13.1 (± 2.8) meters. No single hound was ever beyond 55 meters of the true path of the puma, though the average maximum deviation was 19.1 ± 11.7 meters.

Energetic demands

Across chases, the metabolic rates (kJ·min^{-1}) of pumas during escape (76.5 ± 15.1) were nearly four times higher than those of the pursuing hounds (20.1 ± 15.1, t (6) = 2.65, p = 0.038; Fig. 3.5). On a mass-specific basis, metabolic rates (kJ·kg·min^{-1}) were still > 1.6× greater in pumas relative to hounds (1.29 ± 0.27 vs. 0.76 ± 0.27 kJ·kg·min^{-1}). Similarly, transport costs (J·kg^{-1}·m^{-1}) were >2× as high for pumas (11.7 ± 1.4) than hounds (5.5 ± 1.4, t (6) = 3.05, p = 0.023; Fig. 3.5).

Hounds remained well below their anaerobic threshold (i.e., $\dot{V}O_{2MAX}$) for the duration of all pursuits, with peak hound $\dot{V}O_2$ estimates during the highest-intensity chase (chase 4) of 60 ml O_2·kg^{-1}·min^{-1}, or just 40% of $\dot{V}O_{2MAX}$ (Fig. 3.6). In contrast, pumas routinely exceeded $\dot{V}O_{2MAX}$ during escapes, with an average of 52.5 ± 16% (range: 32-100%) of each escape requiring energy from anaerobic metabolism. Exercise effort was comparatively larger for pumas compared to hounds (Figs. 3.1d, 3.6, S3.2-3.4d) and on average, one minute spent escaping cost pumas 4.64× (± 1.3) as much energy as a typical minute spent actively hunting. In other words, the average puma escape duration of 03:48 (± 01:16) was metabolically equivalent to about 18 minutes of routine, active hunting.

Discussion

In quantifying the fine-scale pursuit and evasion dynamics of two large carnivores, including free-ranging, cryptic pumas, we present evidence for morphological and physiological constraints imposed by specialization towards divergent hunting modes. Though the highly cursorial, endurance-adapted canids (here, scent hounds) exhibited relatively poor maneuverability and maximum speed compared with pumas, these animals maintained lower metabolic rates (Fig. 3.6b) and transport costs (Fig. 3.6d) than their felid "prey." Relatively larger hearts (Williams *et al.* 2015) and greater lung volumes (Kreeger 2003; Murphy & Ruth 2009) provide large canids with wider aerobic scopes (the ratio of $\dot{V}O_{2MAX}$ to $\dot{V}O_{2\,BASAL}$ and an index of aerobic athleticism; Gillooly et al., 2017; Taylor et al., 1987; Weibel et al., 1983) and enhanced endurance capacity compared with felids of comparable size. Skeletal specializations include 'box-like' elbow joints and limbs locked in a more prone position (Figueirido *et al.* 2015), facilitating wolves' ability to travel for several kilometers at 56-64 km·hr^{-1} (Mech 1970; Mech *et al.* 2015a), pursue prey over distances in excess of 20 km (Mech & Korb 1978; Mech *et al.* 2015a), and cover 76 km in 12 hours (Mech & Cluff 2011). As with other social canids, hounds worked together effectively as a pack to detect and maintain each puma's scent while giving chase through steep terrain and dense brush understory.

In contrast, as solitary, highly adapted stalk-and-pounce predators, pumas rely heavily on an element of surprise coupled with a short pursuit ($\leq$ 10 meters, Laundré and Hernández, 2003) before making contact with and subduing prey (Murphy &

Ruth 2009). Compared to canids, in felids, pouncing and grappling with prey are aided by wider elbow joints (Figueirido *et al.* 2015), greater spinal flexibility (Spoor & Badoux 1988; Ruben 2010), and other limb and pelvic adaptations (Taylor 1989). We documented the extreme performance capabilities of this ambush-hunting mode (Table 3.3, Fig. 3.4; also see Williams et al., 2014) as well as the physiological limitations for stamina exacted during the flight response (Figs. 3.5, 3.6). For example, though brief, the maximum puma escape G-force measurements (Fig. 3.3), in excess of ± 5 g, are comparable to those experienced during an Olympic luge race or under maximum braking force in a Formula 1 racecar (Gforces.net 2010). Such peak performance capacity is energetically expensive (Figs. 3.2d, 3.6, S3.2d-3.4d), and each pumas' second escape was much shorter in distance and duration in part due to exhaustion and/or overheating. Our recapture results provide field-based empirical support for the locomotor ramifications of these hunting mode differences between large canids and felids.

Describing species-specific energetic costs and movement ecology can elucidate population-level consequences of anthropogenic disturbance and environmental change (Stephens & Krebs 1986; Gorman *et al.* 1998; Wikelski & Cooke 2006; Somero 2011; Seebacher & Franklin 2012; Cooke *et al.* 2013; Humphries & McCann 2014; Tomlinson *et al.* 2014; Laundré 2014; Scantlebury *et al.* 2014; Wong & Candolin 2014). Cumulative costs associated with exposure to disturbance can tip the energy balance for large carnivores and potentially lead to demographic changes that reverberate through the ecological community (Ripple *et*

al. 2014; New *et al.* 2014; King *et al.* 2015). Here and elsewhere (e.g. Smith et al., 2015; Williams et al., 2014), we show that disturbance and escape costs are high pumas, even when they are not ultimately treed and shot. This result has particular management significance where dogs are utilized in puma hunts (e.g. most Rocky Mountain states) given that sublethal effects may have long-term individual fitness consequences that can negatively impact population dynamics (Preisser, Bolnick & Benard 2005; Peckarsky *et al.* 2008; Gallagher *et al.* 2017).

A recent terrestrial predator-prey pursuit model developed by Wilson et al. (2015) suggested that during predation interactions, the larger animal would be absolutely faster, but have inferior turning ability. Using our accelerometer datasets, we found greater maximum speeds and maneuverability in pumas (weighing over twice the mass of each hound), but slower average speeds. Differences between our findings and predictions of the Wilson et al. model can be explained in part by recognizing our study's violation of several underlying model assumptions. For instance, our recaptures did not occur between a solitary predators pursuing solitary prey on flat and homogenous terrain, nor were the predator(s) and prey geometrically similar. In addition, some differences may be explained by morphological and physiological specialization in canids and felids, as well as local adaptations to rugged topography enhancing momentary escape performance in pumas.

We recognize that our opportunistic hound-assisted puma recaptures constitute semi-natural interactions, but nevertheless their analysis serves as an important first step in understanding the complexities and tradeoffs of locomotor performance *vs.*

energy expenditure in large felids and canids. This approach also serves as a framework for quantifying natural competitive or predatory interactions and their outcomes in the future. Furthermore, we suggest that hound-elicited escapes by pumas may reflect direct interspecific interactions between wolf packs and solitary pumas in sympatric landscapes. While some evidence suggests that pumas are capable of killing subadult (Ruth & Murphy 2009b) and adult wolves (Schmidt & Gunson 1985), the pack hunting strategy of wolves generally makes them dominant competitors against solitary pumas during direct conflicts (Husseman *et al.* 2003; Kortello, Hurd & Murray 2007; Ruth & Murphy 2009b; Ruth *et al.* 2011; Bartnick *et al.* 2013).

Where they coexist, wolves and pumas often exhibit temporal as well as spatial niche partitioning, with pumas often utilizing edge habitat (Laundré & Hernández 2003) or rugged terrain (e.g., steep slopes, boulders) dominated by vegetative cover for concealment when hunting (Logan & Irwin 1985; Laing & Lindzey 1991; Williams, McCarthy & Picton 1995; Jalkotzy, Ross & Wierzchowski 2002; Husseman *et al.* 2003). Wolves, in comparison, tend to prefer valley bottoms and open country (Husseman *et al.* 2003; Alexander, Logan & Paquet 2006; Atwood, Gese & Kunkel 2007; Kortello *et al.* 2007). In addition to being critical for hunting cover (Kleiman & Eisenberg 1973), pumas and other solitary felids rely on structural complexity and vegetative cover as escape terrain during direct intra- and interspecific conflict (Duke 2001; Ruth 2004; Dickson, Jenness & Beier 2005; Kortello *et al.* 2007). Furthermore, trees may serve as primary and immediate refuge

61

from wolves and other threats as pumas do not readily utilize trees for other purposes, such as arboreal prey caching and consumption observed in other felids (e.g., lynx, leopards; Balme et al. In Press; Vander Waal, 1990). We observed this phenomenon in the field; each puma escape was characterized by agile, high-performance maneuvering that terminated with jumping into a tree immediately prior to being overtaken by the hound pack. Maintaining adequate vegetative cover therefore provides a dual concealment-safety benefit to pumas, indicating the importance of protecting complex habitat, in addition to adequate prey, to ensure the long-term persistence of these cryptic predators (Beier 2009; Burdett *et al.* 2010; Wilmers *et al.* 2013; Laundré 2014; Williams *et al.* 2014), especially where they co-occur with wolves (Kortello *et al.* 2007; Ruth & Murphy 2009b; Bartnick *et al.* 2013).

Table 3.1: Comparison of hunting mode divergence observed in large felids and canids. Selected references for each topic (superscripts) are provided below.

	Family *Felidae*	Family *Canidae*
	E.g., puma, leopard, jaguar	E.g., gray wolf, hound, dingo
Hunting mode[a]	Cryptic stalking and pouncing "Surprise and subdue"	Cursorial pursuit "Charge and chase"
Hunting sociality[b]	Solitary	Often group/pack
Relative prey selectivity and timing[c]	Low (opportunistic) Prior to attack	High (selective) Often during pursuit
Interaction with & risk imposed by prey[d]	Short Lower risk of injury/death	Prolonged Higher risk of injury/death
Kill site attributes[e]	Sufficient structural cover for concealment during stalking and brief pursuit	Relatively open terrain that facilitates prolonged pursuit
Scale of habitat features impacting hunt success[f]	Small-scale habitat features	Large-scale landscape heterogeneity
Relative activity and energetic demand of hunt's attack phase	High intensity, short duration	Low intensity, long duration

[a]Hornocker, 1970; Koehler and Hornocker, 1991; Ruth and Murphy, 2009a; Seidensticker et al., 1973; Young, 1946; Poole and Erickson, 2011; Snow, 1985; Mech and Korb, 1978; Mech and Cluff, 2011
[b]Gittleman, 1989; Hornocker and Negri, 2009; Mech et al., 2015; Mech, 1970
[c]Husseman et al., 2003; Wilmers et al., 2007; Kunkel et al., 1999; Okarma et al., 1997; Mech et al., 2015; Peterson and Ciucci, 2003; but see Karanth and Sunquist, 1995; Krumm et al., 2010
[d]Hornocker and Negri, 2009; Mech et al., 2015; Mech and Boitani, 2003
[e]Alexander et al., 2006; Hebblewhite and Merrill, 2008; Husseman et al., 2003; Ruth et al., 2011; Schmidt and Kuijper, 2015 and references therein
[f]Hebblewhite et al., 2005; Kauffman et al., 2007; Laundré and Hernández, 2003; Podgórski et al., 2008; Schmidt and Kuijper, 2015

Table 3.2: Summary of pursuit and escape parameters from hounds and pumas, respectively. Measurement units are enclosed in parentheses. Average speed (m·s^{-1}) is GPS- rather than accelerometer-derived, and across-chase averages (± s.e.m) are presented.

	Hounds (n)	Hound Distance (m)	Duration (mm:ss)	Avg. Speed (m·s^{-1})	Elev. Gain/Loss (m)	Puma Distance (m)	Duration (mm:ss)	Avg. Speed (m·s^{-1})	Elev. Gain/Loss (m)
Chase 1	5	1270	07:37	2.78	228/-161	482	06:56	1.16	121/-84
Chase 2	5	1400	15:13	1.53	306/-157	178	02:48	1.06	70/-32
Chase 3	4	1120	12:08	1.54	99/-339	363	04:15	1.33	88/-139
Chase 4	4	291	00:59	4.93	80/-75	316	00:57	5.54	89/-110
Average		1020 (250)	08:39 (03:05)	2.7 (0.8)	178 (54) -183 (56)	334.8 (62.8)	03:44 (01:15)	2.27 (1.09)	92 (11) -91 (23)

Table 3.3: Average (± s.e.m.) chase tortuosity and speed performance during hound-assisted puma recaptures. Average and maximum speeds ($m \cdot s^{-1}$) are presented for both GPS and accelerometer-derived estimates. Sample sizes and measurement units are enclosed in parentheses, and results from Welch two-sample t-tests comparing hound and puma data are included.

Chase	Species (animals)	Tortuosity	GPS Speed ($m \cdot s^{-1}$)		Accel. Speed ($m \cdot s^{-1}$)	
			Avg.	Max.	Avg.	Max.
1	Hounds (n=5)	2.01±0.08	2.33±0.09	8.53±0.29	3.07±0.07	5.2
	Puma 36M	2.22	0.93±0.21	5.27	3.69±0.27	14.5
			t = -6.5		t = 2.3	
			p < 0.01*		p = 0.02*	
2	Hounds (n=5)	3.61±0.21	1.53±0.03	7.5±0.45	2.43±0.05	5.93
	Puma 36M	3.34	0.56±0.17	2.89	3.49±0.34	15.0
			t = -6.4		t = 3.1	
			p < 0.01*		p < 0.01*	
3	Hounds (n=4)	1.98±0.09	1.35±0.04	5.5±0.87	3.32±0.06	6.4
	Puma 26M	4.95	0.48±0.11	2.38	2.85±0.2	11.8
			t = -8.7		t =-2.2	
			p < 0.01*		p = 0.03*	
4	Hounds (n=4)	1.42±0.06	3.04±0.2	5.89±0.45	5.35±0.15	6.35
	Puma 26M	1.15	2.32±0.51	3.86	11.06±0.5	14.49
			t = -1.4		t = 12.1	
			p = 0.16		p < 0.01*	
Avg.	Hound	2.32±0.24	1.7±0.03	7.0±0.38	3.89±0.18	5.97±0.28
	Puma	2.92±0.52	0.74±0.09	3.6±0.63	2.94±0.04	13.9±0.73
		t = 1.04	t = -10.4	t = -3.9	t = 5.2	t = 10.3
		p = 0.31	p < 0.01*	p < 0.01*	p < 0.01*	p < 0.01*

*Denotes significant relationship ($p \leq 0.05$)
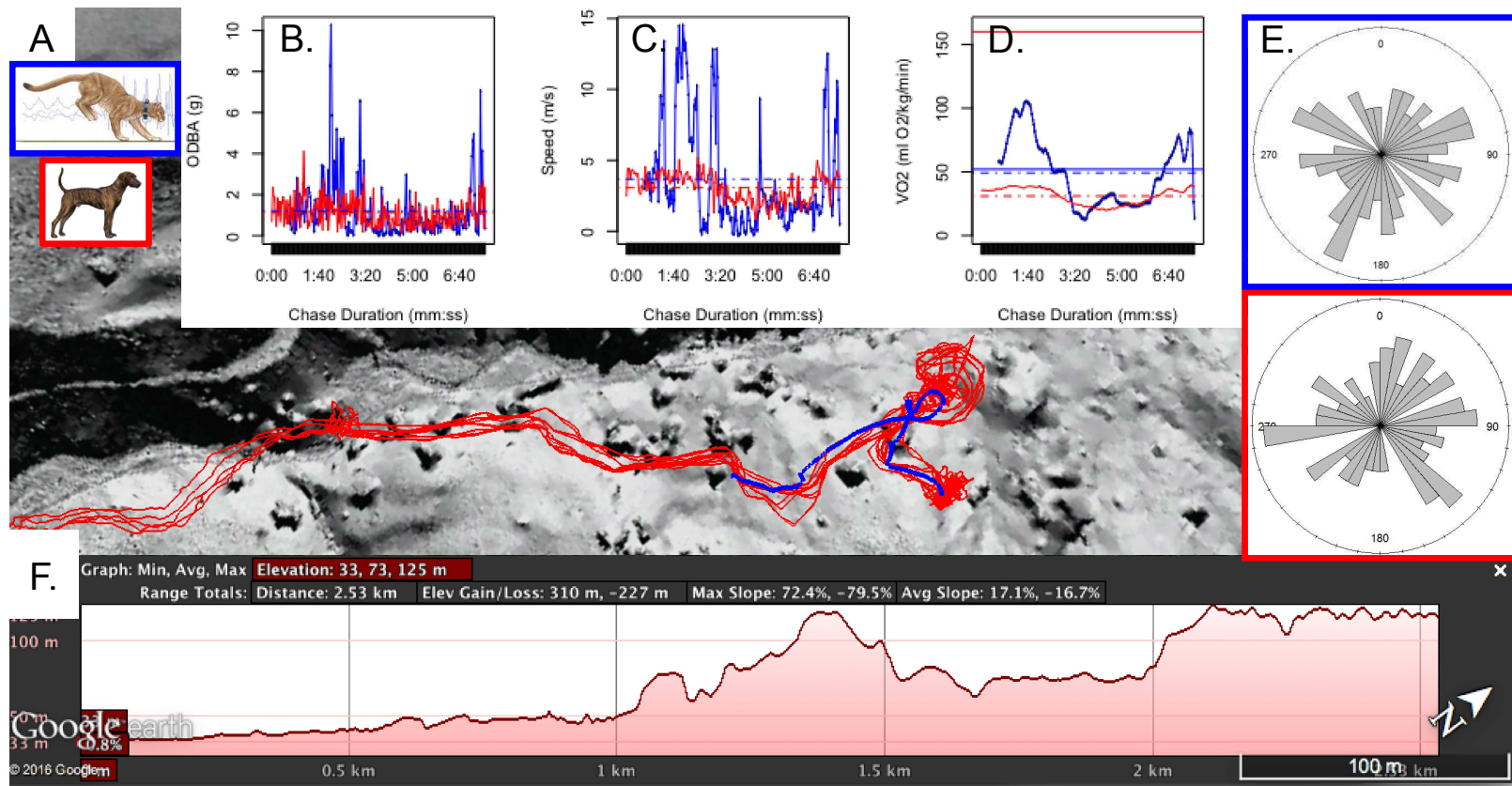
Figure 3.1: Chase 1 pursuit (red lines = hounds) and escape (blue line = puma) paths (A), including the elevation profile for Brandy, the GPS-accelerometer collar equipped hound. Insets display ODBA (g, B), speed (m·s⁻¹, C), and estimated mass-specific metabolic demand ($\dot{V}O_2$ in ml O_2·kg⁻¹·min⁻¹, D) For B, C, and D, mean values are presented as dashed horizontal lines, and solid horizontal lines in D. depict $\dot{V}O_{2\ MAX}$ for each species. Tortuosity plots (proportion of turns in each compass direction, E) and the elevation profile for the accelerometer-GPS-equipped hound (F) are also presented.
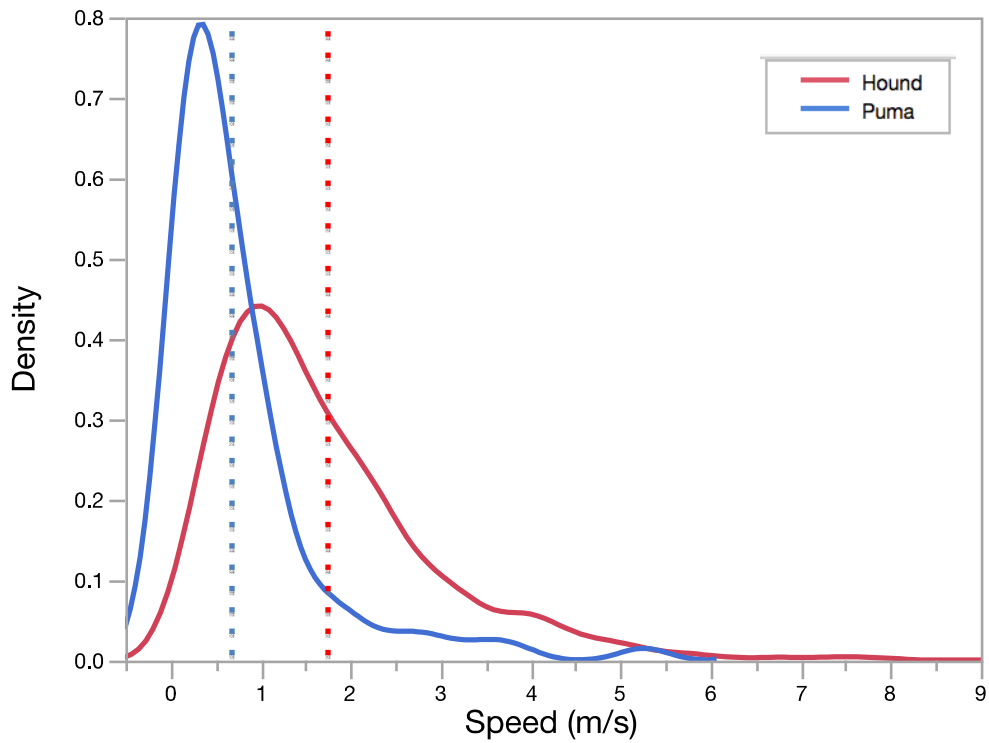
Figure 3.2: GPS-derived pursuit and escape speeds for hounds (red) and pumas (blue), respectively, during all chases. The mean (± s.e.m.) speeds, in m/s, for hounds (1.7 ± 0.03) and pumas (0.74 ± 0.09) are depicted as dashed vertical lines.
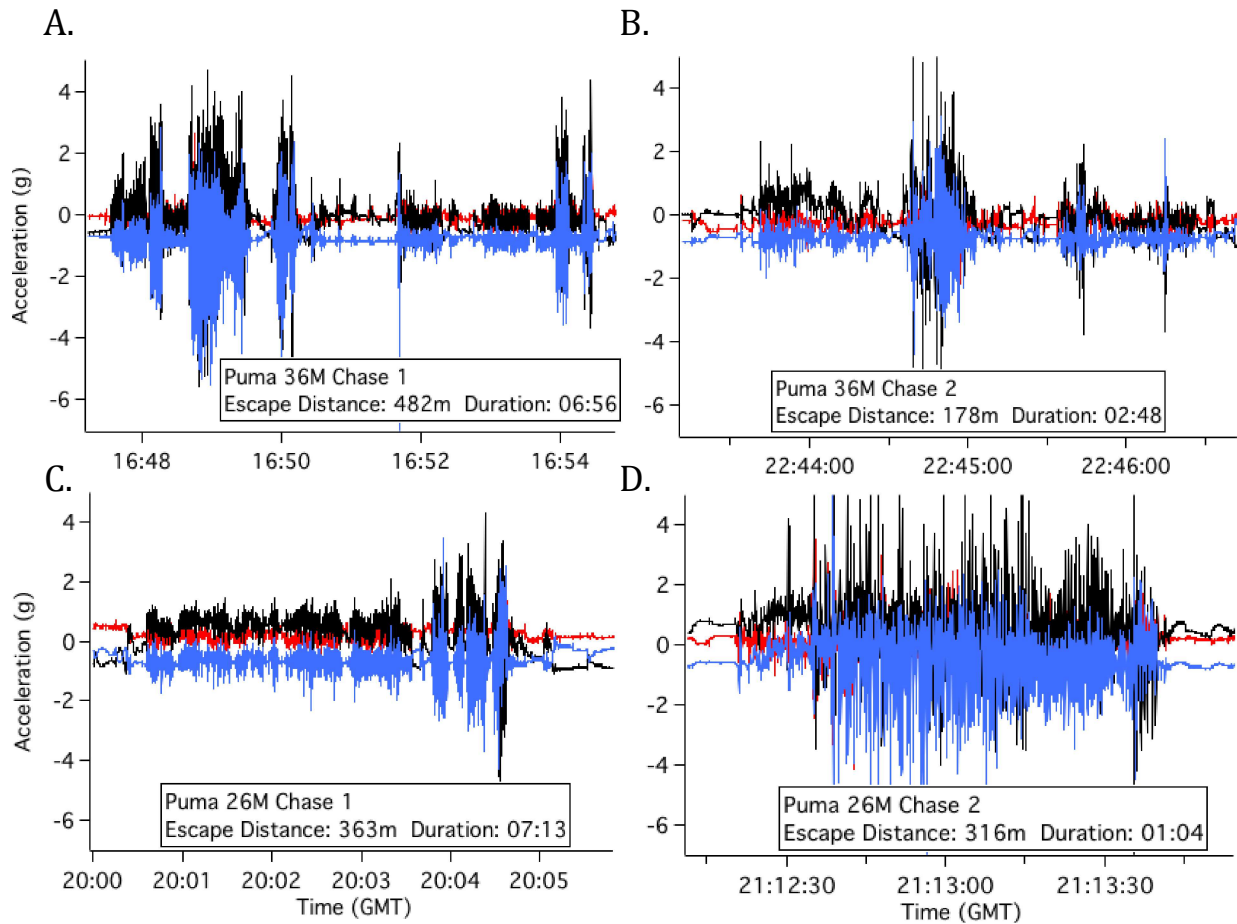
Figure 3.3: Escape acceleration signatures of adult male pumas 36 (A, B) and 26 (C, D). Acceleration (g) is scaled to the same range for comparison. Chase distance is in m and chase duration is in mm:ss. Colors correspond to pumas' accelerometer-GPS collar orientation in the X (transverse sway, black), Y (anterior-posterior surge, blue), and Z (dorsal-ventral heave, red) planes.
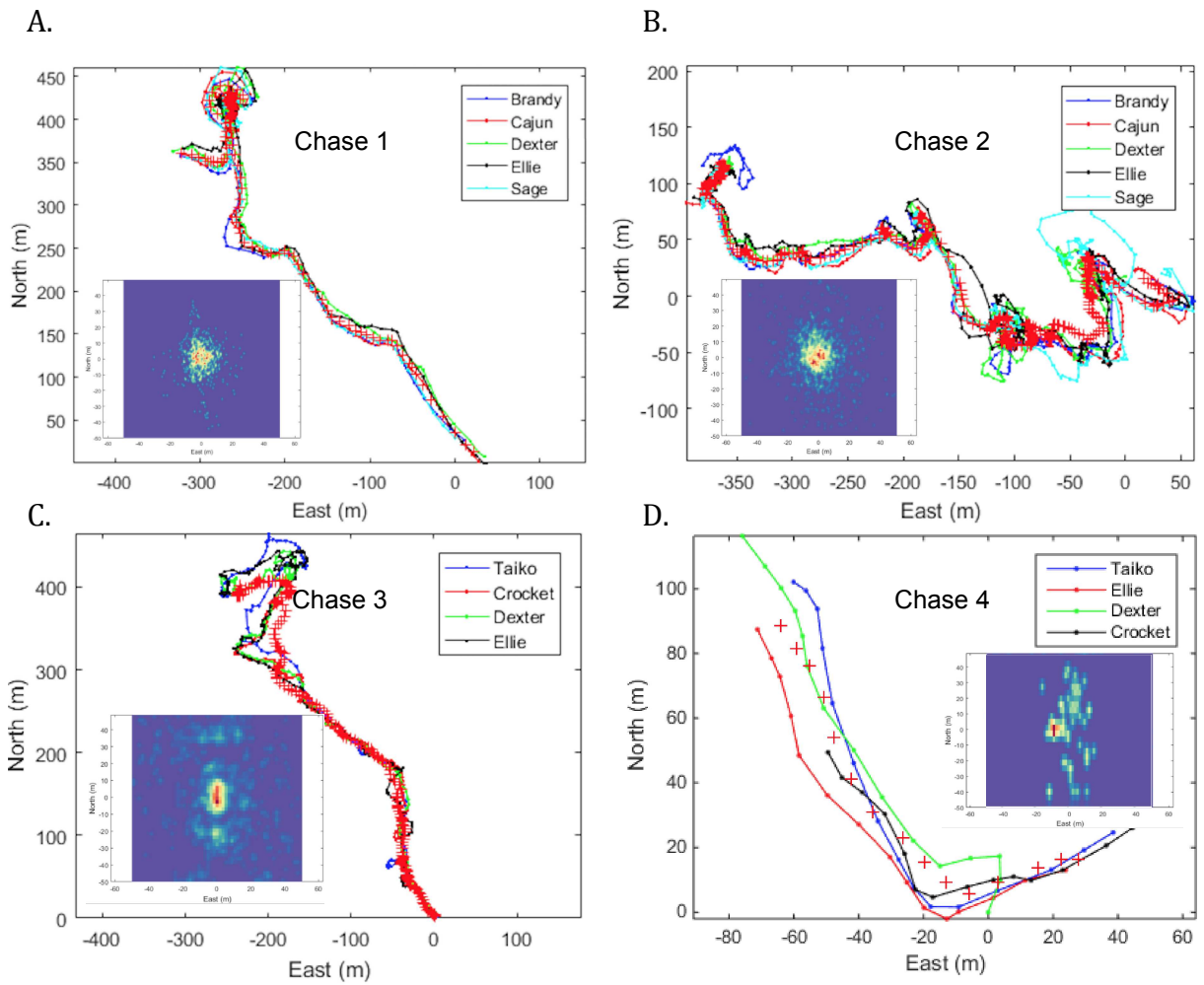
Figure 3.4: Hound pursuit paths (A-D) and 2D-spatial histograms (E-H) of pack cohesion over the course of each chase. The group centroid throughout each pursuit path is marked as a red plus (+). In the spatial histogram insets, the relative position of each hound relative to the group centroid is scaled by color, with warm colors representing close group cohesion and cool colors depicting more distant spacing.
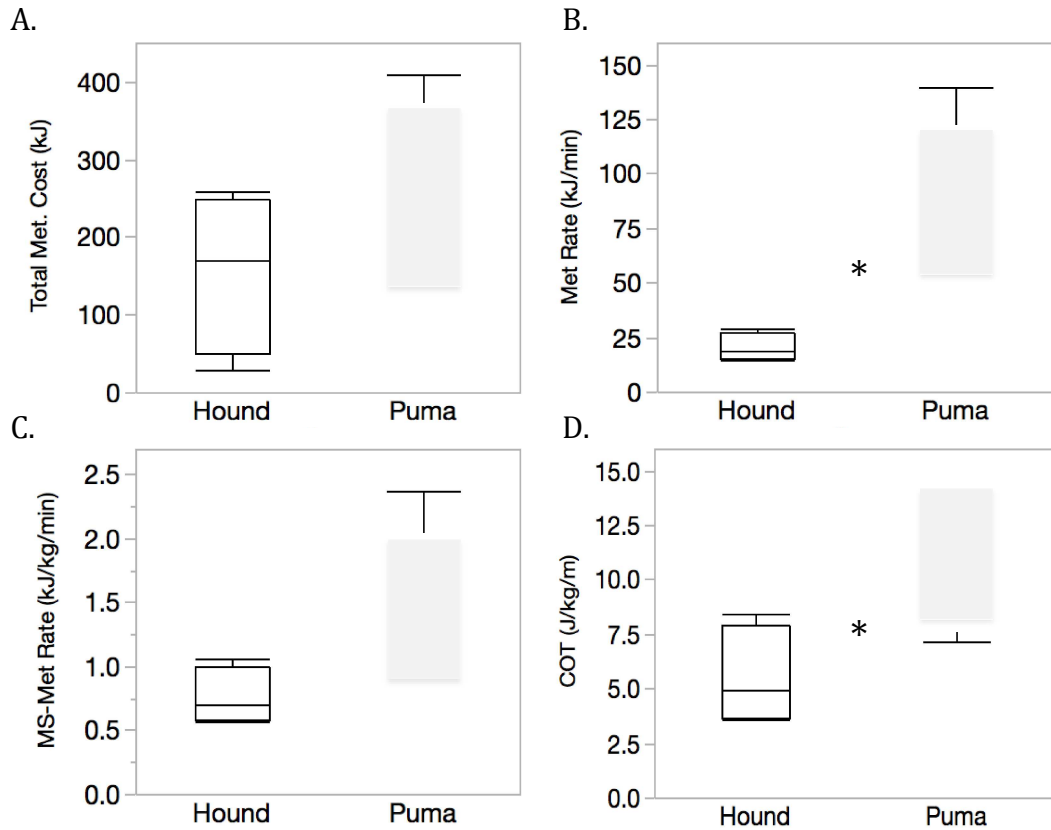
Figure 3.5: Energetic costs of pursuit and evasion for hounds (white) and pumas (grey), respectively, summarized across four chases. Total metabolic cost (kJ, A), metabolic rate (kJ·min^{-1}, B), mass-specific metabolic rate (kJ·kg^{-1}·min^{-1}, C), and cost of transport (COT, J·kg^{-1}·m^{-1}, D) are shown. Asterisks (*) denote significant ($p \leq 0.05$) differences between species.
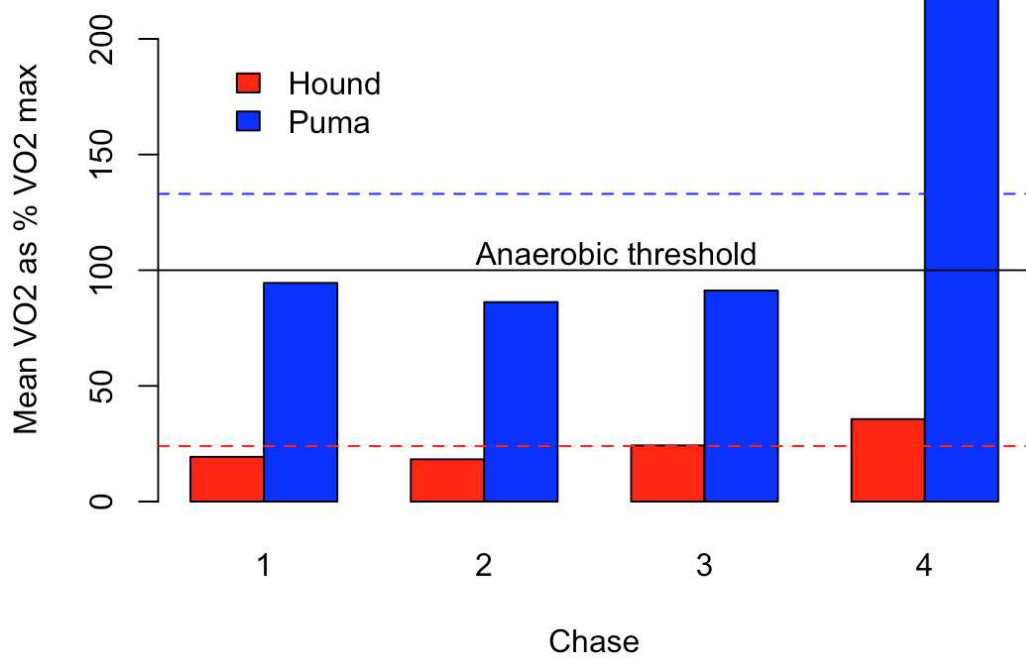
Figure 3.6: Estimated mean metabolic rate ($\dot{V}O_2$, ml $O_2 \cdot kg^{-1} \cdot min^{-1}$) expressed as a percentage of $\dot{V}O_2$ MAX for hounds (red) and pumas (blue) during each chase.

SUPPLEMENTARY MATERIALS
CHAPTER 3

Videos S3.1-4: Chase reconstructions visualized in Google Earth Pro are available upon request to the author.
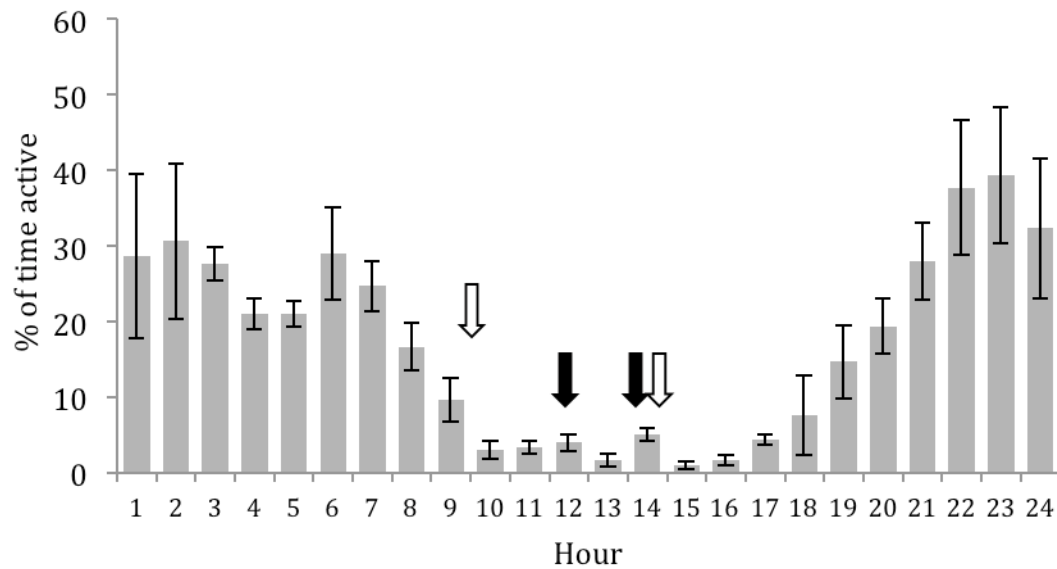
Figure S3.1: Predicted average hourly activity across a 24-hour period for male pumas (± s.e.m.) in the Santa Cruz Mountains, CA. Arrows correspond to the time of day in which chases for recapture occurred. White arrows show the timing of chases for male puma 36 on Aug. 3, 2015, and black arrows show the timing of chases for male puma 26 on Nov. 18, 2015. Daily activity estimates are averaged across 2 weeks from each of three adult male pumas (Wang et al., 2015b).
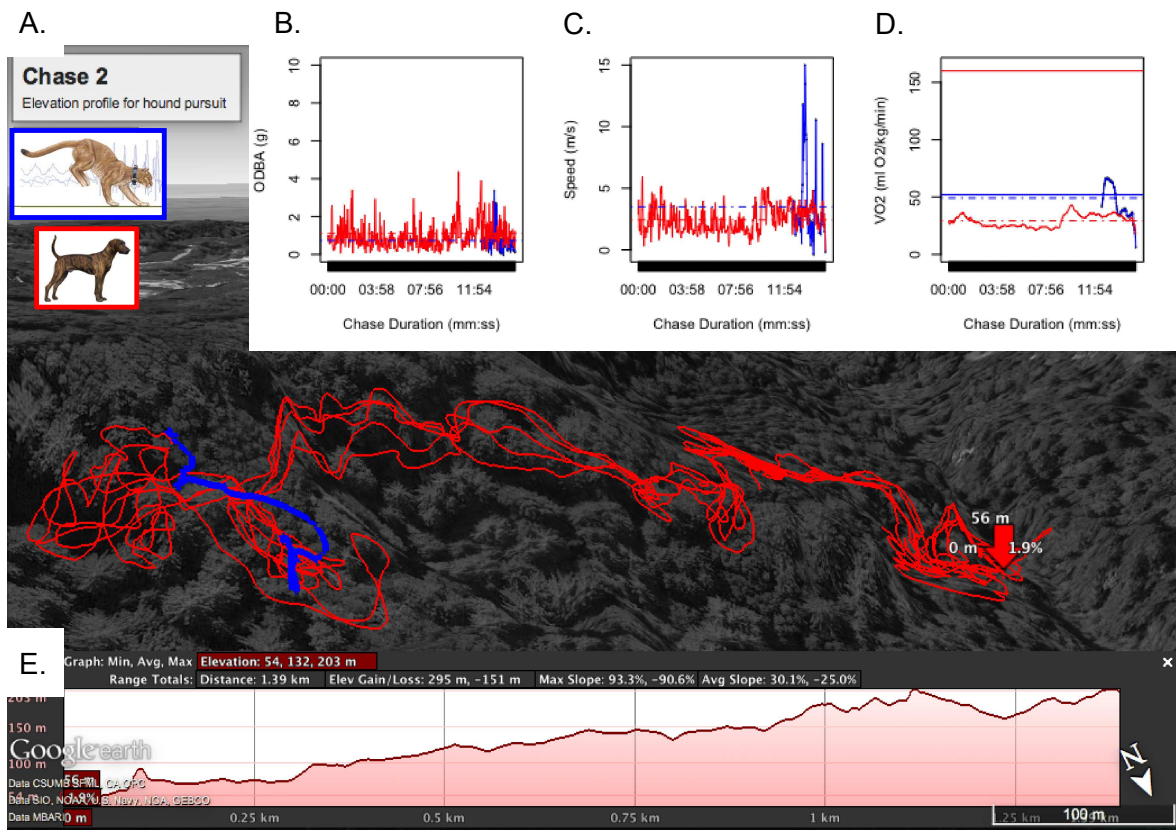
Figure S3.2: Chase 2 pursuit (red lines = hounds) and escape (blue line = puma) paths and parameters. Insets display ODBA (g, B), speed (m·s⁻¹, C), and estimated mass-specific metabolic demand ($\dot{V}O_2$ in ml O_2·kg⁻¹·min⁻¹, D.) For B, C, and D, mean values are presented as dashed horizontal lines, and solid horizontal lines in D. depict $\dot{V}O_{2\ MAX}$ for each species. The elevation profile (F) for the accelerometer-GPS-equipped hound is also presented.
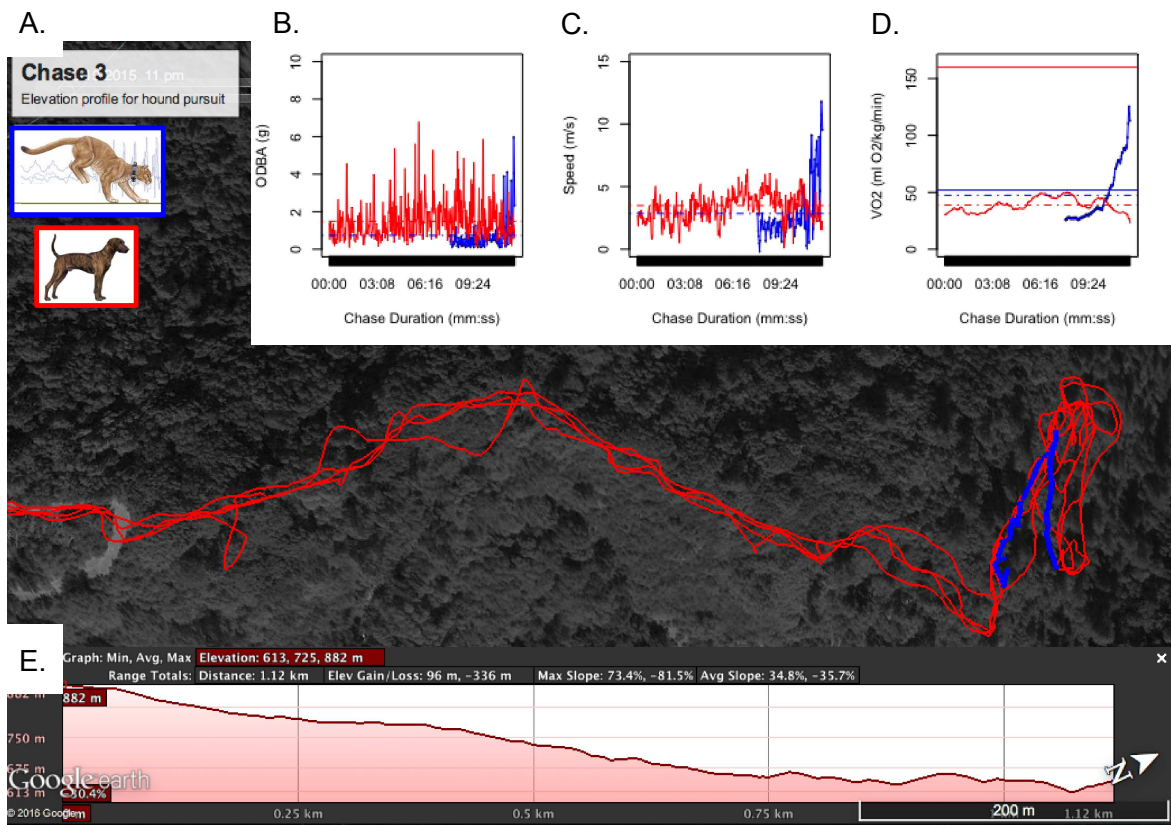
Figure S3.3: Chase 3 pursuit (red lines = hounds) and escape (blue line = puma) paths and parameters. Insets display ODBA (g, B), speed (m·s⁻¹, C), and estimated mass-specific metabolic demand ($\dot{V}O_2$ in ml O_2·kg⁻¹·min⁻¹, D) For B, C, and D, mean values are presented as dashed horizontal lines, and solid horizontal lines in D depict $\dot{V}O_2$ MAX for each species. The elevation profile (F) for the accelerometer-GPS-equipped hound is also presented.
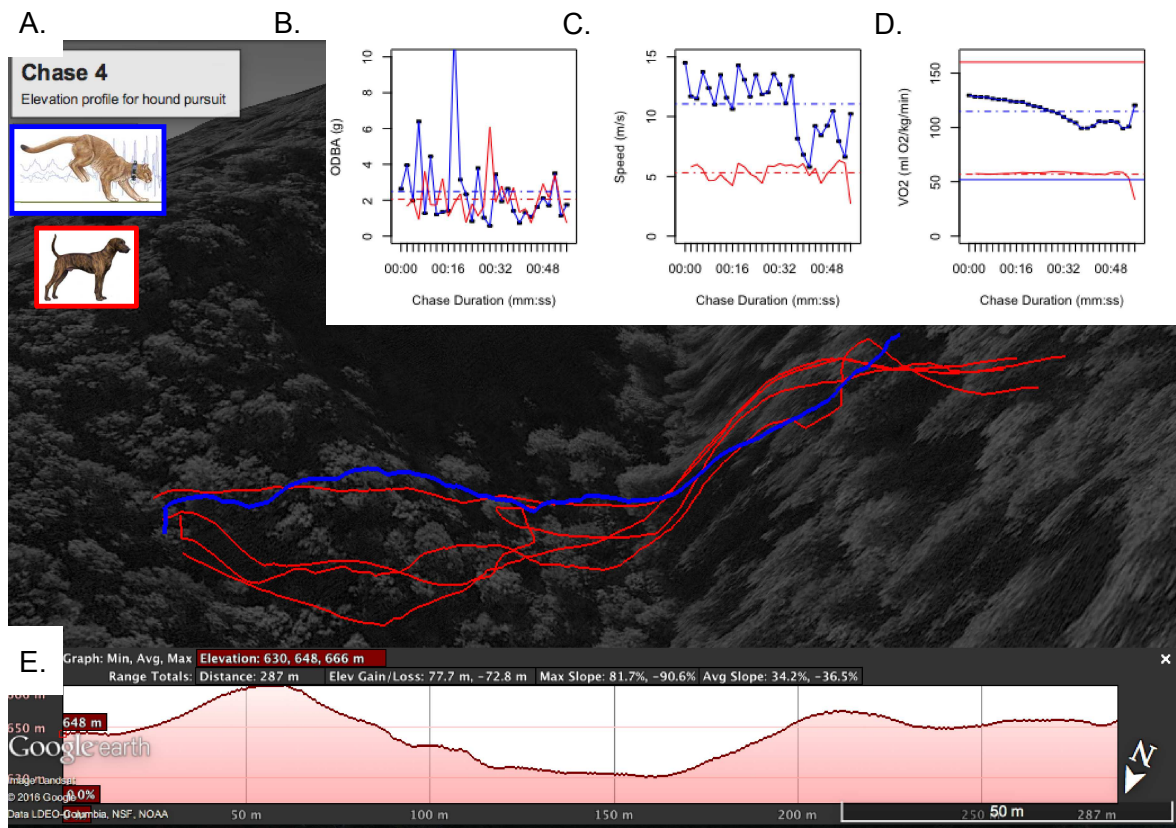
Figure S3.4: Chase 4 pursuit (red lines = hounds) and escape (blue line = puma) paths and parameters. Insets display ODBA (g, B), speed (m·s⁻¹, C), and estimated mass-specific metabolic demand (V̇O₂ in ml O₂·kg⁻¹·min⁻¹, D) For B, C, and D, mean values are presented as dashed horizontal lines, and solid horizontal lines in D. depict V̇O₂ MAX for each species. The elevation profile (F) for the accelerometer-GPS-equipped hound is also presented.

CHAPTER 4

The effects of habitat heterogeneity, season, and reproductive status on male wolf movements and energetics

Abstract

Most environments are dynamic in nature, driving many animals to move to meet their fundamental needs. Such movement is reliant upon metabolic energy, the fundamental currency of ecology. Yet quantifying the activity patterns and energy demands of large carnivores such as gray wolves (*Canis lupus*) in the wild has been historically difficult, resulting in an incomplete understanding of the interplay between physiological and environmental factors that affect animal movement and foraging success. To gain insight into the behaviors, travel patterns, and daily energetic expenditures (DEE) of a keystone predator, we deployed accelerometer-GPS collars on 5 free-ranging adult male wolves in Denali National Park and Preserve (DNPP) for 8 months. GPS data from an additional 14 concurrently monitored wolves (9 packs total) were used to assess how wolf movement patterns and densities varied with habitat and prey heterogeneity along the northern extent of the Alaska Range. Wolves occupying habitat that supports salmon but few large

ungulates (western region) had the highest average DEE (19,042 kJ·wolf^{-1}), the lowest within-pack wolf densities (4.7 wolves·1000 km^{-2}), and the smallest average pack size (2.7 wolves·pack^{-1}) relative to central and eastern DNPP, which has abundant ungulate prey (4.8 wolves·1000 km^{-2} with 6.6 wolves·pack^{-1}, and 8.4 wolves·1000 km^{-2} with 5.3 wolves·pack^{-1}, respectively). On average, wolves in central DNPP traveled significantly farther each day (21 km·day^{-1}) than conspecifics to the west or east (17.3 km·day^{-1} each), presumably to track highly mobile caribou that seasonally migrate through this region. Wolves walked or ran approximately 10% of each day, and both movement rates and DEE in successful male breeders were the same as that of unsuccessful breeders (~17,460 kJ·wolf^{-1}). Identifying such patterns is a critical step towards evaluating how seasonality and heterogeneous prey distribution impact space use and energy allocation in carnivores with ecosystem-wide cascading effects.

Introduction

Habitat selection by animals is dynamic and driven by a suite of factors, yet fundamentally species move through their environments to maximize energy intake while minimizing costs. For grey wolves (*Canis lupus*) and other large carnivores, daily survival depends on balancing the energy gained by resource acquisition (i.e. prey capture) with the energy lost to a variety of costly vital functions (e.g. metabolic work and activity, thermoregulation, growth, reproduction, repair, and waste; Kleiber 1961; McNab 2002; Withers *et al.* 2016). As the currency of ecosystem function,

energetic demand ultimately underlies the behavioral decisions animals make, driving where and how often they feed (Stephens & Krebs 1986; Speakman 2000; Brown *et al.* 2004; Humphries & McCann 2014). The drive for predation in wolves can trigger both density and behaviorally-mediated trophic cascades by directly decreasing prey populations and indirectly impacting the behavior of herbivores (Ripple & Beschta 2004; Christianson & Creel 2014; Creel *et al.* 2015; Ripple *et al.* 2015) and sympatric mesopredators (Levi & Wilmers 2012; Ripple *et al.* 2013; Newsome & Ripple 2014; Wang *et al.* 2015a).

Because these effects propagate downward through food webs (Hairston *et al.* 1960; Paine 1980; Terborgh & Estes 2010), large carnivore abundance and distribution are often incorporated in the design of reserves and protected habitats (Simberloff 2003; Ray *et al.* 2005; Estes *et al.* 2011; Ordiz *et al.* 2013). Given the global decline in many of these keystone species (Morrison *et al.* 2007; Ripple *et al.* 2014; Di Minin *et al.* 2016), the quantification of free-ranging behaviors and resulting energy demands is integral for defining predator resource requirements and establishing critical habitats and corridors for conservation (Berger-Tal *et al.* 2011; Wilmers *et al.* 2013; Laundré 2014; Williams *et al.* 2014). Indeed, describing species-specific energetic costs and movement ecology can elucidate population-level consequences of anthropogenic disturbance and environmental change (Stephens & Krebs 1986; Gorman *et al.* 1998; Wikelski & Cooke 2006; Somero 2011; Seebacher & Franklin 2012; Cooke *et al.* 2013; Humphries & McCann 2014; Tomlinson *et al.* 2014; Laundré 2014; Scantlebury *et al.* 2014; Wong & Candolin 2014).

In large carnivores, the energy demands associated with movement can account for substantial portions of the daily energy budget (Schmidt-Nielsen 1972; Garland 1983; Tatner & Bryant 1986; Boisclair & Leggett 1989; Karasov 1992; Gorman *et al.* 1998; Steudel 2000; Girard 2001; Weibel *et al.* 2004; Rezende *et al.* 2009; Scantlebury *et al.* 2014). As hypercursorial hunters (having specialized morphological and physiological adaptations to running), wolves must locate, pursue, and kill fleeing prey in order to survive (Peterson & Ciucci 2003; Miquelle *et al.* 2005; Mech *et al.* 2015a). To obtain prey and maintain territories, wolves roam widely on a daily basis (Mech 1970), often utilizing natural and anthropogenic linear travel corridors (James & Stuart-Smith 2000; Whittington, St. Clair & Mercer 2005; Latham *et al.* 2011). This enables them to increase prey encounter rates (McPhee, Webb & Merrill 2012) while visiting much of their home range within 1-3 weeks (Jedrzejewski *et al.* 2001). In some cases, wolves have been observed chasing prey for over 20 km (Mech & Korb 1978) and covering nearly 80 km in 12 hours (Mech & Cluff 2011). The costs of these extensive movements are superimposed on intrinsically elevated energy demands associated with large body size (Peters 1983), endothermy (Bennett & Ruben 1979), and carnivory (Carbone *et al.* 2007, 2011), suggesting a key selective advantage for minimizing locomotor costs (Okarma & Koteja 1987; Bryce & Williams 2017).

Both abiotic (e.g. snow, disturbance) and biotic (e.g. prey movement and vulnerability) factors affect wolf movement decisions and hunting patterns (e.g. Peterson & Allen 1974; Huggard 1993; Thurber & Peterson 1993; Dale, Adams &

Bowyer 1994; Hayes *et al.* 2000), and to keep costs down, wolves often behaviorally minimize energy expenditure associated with travel. For example, wolves often select linear travel corridors, whether anthropogenic (e.g. roads, seismic lines; Whittington *et al.* 2005; Latham *et al.* 2011; Dickie *et al.* 2016) or natural (e.g. frozen rivers through riparian habitat preferentially selected for willow browsing by moose; Renecker & Schwartz 1997; Baigas *et al.* 2010; McPhee *et al.* 2012). When traveling through deep snow, wolves frequently travel in single file, presumably to conserve energy (Liberga *et al.* 2012). Nevertheless, wolf maximum energetic demands exceed those of comparably sized placental mammals by a factor of three (Lechner 1978; Seeherman *et al.* 1981; Weibel *et al.* 1983, 2004; Okarma & Koteja 1987; Taylor *et al.* 1987a), which suggests that wolves, like other large carnivores, may be routinely working close to their maximum sustained energetic outputs (Gorman et al. 1998; Scantlebury et al. 2014).

Daily energy requirements may be particularly high for dominant individuals (e.g. breeders) in the pack, which travel extensive distances to obtain food for their pups (Jedrzejewski *et al.* 2001; Mech & Cluff 2009), as well as lead and press attacks on prey during hunts (Murie 1944; Haber 1977; Ballard, Whitman & Gardner 1987; Mech 1988). Dominant breeding wolves also spend the most time in frontal leadership as the pack is traveling (Peterson *et al.* 2002), which can be particularly demanding when breaking trail for the pack through thick vegetation or snow (Steudel 2000; Murray & Lariviere 2002; Crête & Larivière 2003). As such, they may be vulnerable to environmental perturbations that increase activity or decrease prey

availability, which can upset the energy balance (Gorman *et al.* 1998; Carbone *et al.* 2007; Laundré 2014; Scantlebury *et al.* 2014). Despite the crucial role that dominant wolves play in pack persistence (Mech & Boitani 2003b; Borg *et al.* 2015), the free-ranging activity patterns and associated energy budgets for these animals remain poorly understood (Peterson & Ciucci 2003).

Measuring the fine-scale behavior and field physiology of large carnivores has been a long-standing challenge since these predators occur at low densities, range widely, and often avoid human-modified landscapes (e.g. Gese 2001; Thompson 2004; Ripple *et al.* 2014). To date, most estimates of mammalian energetics are coarse, cumulative values of field metabolic rate (FMR) derived from doubly-labeled water studies over weekly timescales (Speakman 1997; Halsey 2011). Free-ranging wolf metabolic rates (and hence prey demands) have been modeled and estimated based on basal metabolism (Weiner 1989; Glowacinski & Profus 1997; Peterson & Ciucci 2003), but rarely empirically measured (Swain, Costa, and Mech, cited in Nagy 1994). Recent advancements and miniaturization of biologging sensor technology, however, enable scientists to concurrently measure previously unavailable metrics including the behavior, physiological performance, and energetics of wild animals at near-instantaneous scales across seasons or even years (Williams *et al.* 2014; Kays *et al.* 2015; Wilmers *et al.* 2015)

Here, using GPS-equipped accelerometer collars, we examined 8 months of movement patterns, activity budgets, and energy expenditure in dominant male wolves across a topographic and ungulate prey gradient in interior Alaska. We

predicted that daily travel distance and daily energy expenditure (DEE) would be lowest in fall for wolves in western Denali National Park and Preserve (DNPP) due to the seasonal availability of Pacific-run salmon in this region (Adams *et al.* 2010). We also evaluated two competing hypotheses concerning the impact of pack reproductive status on adult male wolf energy expenditure. If prey is abundant, reduced hunting costs may mean that successful breeders expend less energy than conspecifics in packs that fail to reproduce successfully. Conversely, if demands associated with providing for young are high, successful breeders may expend more energy than conspecifics not provisioning for pups. To evaluate these hypotheses, we compared regionally specific activity patterns and metabolic demands of free-ranging wolf packs that did and did not rear pups in 2015. Finally, we utilized seasonal DEE to estimate ungulate-specific minimum prey requirements for wolves, and discuss these results in the broader ecological context in DNPP, namely regional variation in habitat type and prey available to wolves.

Methods

Behavioral & energetic calibrations

We used a laboratory-to-field approach (e.g., Williams *et al.* 2014; Wang *et al.* 2015; Wilmers *et al.* 2015) in which the routine behaviors and locomotor biomechanics of captive wolves (n=2 adults, 1M, 1F; avg. mass = 39 kg) instrumented with accelerometer-Global Positioning System radiocollars (hereafter Acc.-GPS collars) were measured in an outdoor enclosure prior to deployment on

free-ranging conspecifics in the wild. We paired video-recorded observations of captive wolves performing routine activities (e.g. resting, feeding, interacting, traveling) with accelerometer measurements to build a classification algorithm for categorizing those behaviors from wild conspecifics. Each wolf wore an integrated Acc.-GPS collar (GPS Plus, Vectronic Aerospace, Germany; approx. 960 g) that sampled acceleration continuously at 32Hz and took hourly relocation fixes via GPS satellites. The tri-axial accelerometer (± 8 g range) was mounted such that the X-, Y-, and Z-axes were parallel to the anterior-posterior ("surge"), the dorsoventral ("heave"), and transverse ("sway") planes of the animal, respectively (Fig. 4.1a).

For each locomotor gait, basic stride mechanics (speed, stride frequency, and stride length) and overall dynamic body acceleration (ODBA) were measured as each wolf was filmed (Sony HDR-CX290/B, 1080 HD, 60p) moving freely at known speeds behind a vehicle and along a fence line between trainers in large (> 1 acre) outdoor enclosures (Fig. 4.1b,c). Following the captive wolf locomotor trials, collared individuals were filmed continuously for 2-3 hours while behaving naturally without human interaction to validate that the accuracy and field relevance of the data obtained during locomotion trials. Downloaded accelerometer signatures were annotated from video recordings on a per second basis to construct a training dataset for our behavioral classification model. Both speed and metabolic rate are tightly linked to the dynamic component of an animal's body acceleration (Wilson *et al.* 2006; Gleiss *et al.* 2011; Bidder *et al.* 2012a; b; Qasem *et al.* 2012), allowed us to use

wolf ODBA to translate sensor output from the collars into travel speed and the

metabolic demands of various activities in the wild.

Behavioral classification

Utilizing random forest (RF) supervised machine-learning algorithms, we

classified captive wolf observations using a simple mobility model (active *vs*. resting)

as well as a more detailed behavioral model, which discriminated 5 behaviors (rest,

locomotion, eat, active, and sleep). These RF models enabled us to predict

unobserved behaviors at coarse and finer scales, and then reconstruct activity budgets

from Acc.-GPS equipped free-ranging wolves based on measurements of observed

behaviors in captive wolves. Because wild wolves were tranquilized during capture,

we excluded behaviors on the days of collar deployment and retrieval since wolf

activities on these days were not representative of wild behavior. Standing, sitting,

and lying down were classified as resting behaviors, and locomotion included

trotting, loping, and galloping gaits (Table S4.1).

We linked behaviors of interest to their corresponding accelerometer data,

then converted raw accelerometer values to units of gravity (1 g = 9.81 m·s^{-2}). Static

(i.e. gravitational) acceleration was subtracted from raw acceleration using a 2 second

running mean to calculate dynamic acceleration caused by the movement of the

animal (Wilson *et al.* 2006; Shepard *et al.* 2008b). Using R (v. 3.1.1; R Core Team

2014), we then derived 10 parameters from the accelerometer data over 2 second

intervals (Table S4.2). These predictors were selected based on their utility in

classifying behavior from previous studies (e.g. Nathan *et al.* 2012; Shamoun-Baranes *et al.* 2012; Wang *et al.* 2015; Pagano *et al.* 2017) and had variable importance in the classification accuracy of each model (Fig. S4.1). Wolf behaviors were then predicted using RF modeling (Breiman 2001) implemented in R (RandomForest package). We fit 500 classification trees to our training dataset and used a random subset of 3 predictor variables for each split in the tree.

Collar Field Deployments

Study Area

The DNPP study area (63° N, 151° W; Fig. 4.2) encompasses roughly 16,000 km^2 of boreal forest, gravel river bars, willow-lined creeks, and high alpine habitat patches north of the Alaska Range crest (150-3,000 m in elevation). With a single park road bisecting the northern extent of DNPP, wolf pack territories are largely inaccessible and there is little effect of human harvest of wolves within the park (Adams et al. 2010; but see Borg et al. 2015, 2016) As such, DNPP presents a unique opportunity to study the fine-scale behavior, movement ecology, and predator-prey interactions of an apex carnivore in a relatively un-manipulated ecosystem. Large-scale landscape heterogeneity has been shown to shape wolf movement and predation patterns (Hebblewhite *et al.* 2005; Kauffman *et al.* 2007). Denali's expansive landscape is characterized by a marked west to east transition from relatively homogenous lowland black spruce (*Picea mariana*) forests (western region) to more diverse upland (central region) and predominantly alpine (eastern region) ecosystems,

accompanied by a similar gradient in wolf prey types and densities (Fig. 4.3). The western lowlands support ungulates at low densities (primarily moose, *Alces alces,* the main prey base for wolves in Denali; Mech *et al.* 1995, 1998), as well as Pacific salmon (*Oncorhynchus* spp.) which can constitute a substantial portion of the seasonal diets of wolves in this region (Mech *et al.* 1998; Adams *et al.* 2010). In contrast, the central and eastern portions of the study area support few to no salmon, respectively, but host relatively abundant Dall sheep (*Ovis dalli*) and moose populations (Adams *et al.* 2010), and well as seasonally high densities of caribou (*Rangifer tarandus;* Mech *et al.* 1998; Adams & Roffler 2010). In addition to wolves, predators of ungulates in the study area include grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), lynx (*Lynx canadensis*), wolverines (*Gulo gulo*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*; Sheldon 1930; Mech *et al.* 1998)

The climate in DNPP is subarctic and characterized by short, cool summers. During our 1 March-31 October 2015 study window, average temperatures ranged from -8°C in March to 12°C in July and were 1°C warmer than the 1981-2010 average (Central Alaska Network 2015). Over half of the annual precipitation (38 cm) falls during the summer months, although our study period was considerably wetter (4 cm) than normal (Western Regional Climate Center 2016). No significant multi-decadal trend in annual snowfall at the park headquarters exists, but winter 2014-2015 snowfall was lighter than normal (Central Alaska Network 2015). Snow cover during the Acc.-GPS collar deployment was generally absent from late April through

August, melting sooner but also returning sooner in the year than typical (Central

Alaska Network 2015).

Wolf Movement Ecology

Five adult (2-4 yr old) male gray wolves were captured in March 2015 using

aerial darting by helicopter (Meier & Burch 2009) and anesthetized with zolazepam-

tiletamine (Telazol®, Fort Dodge Laboratories, Fort Dodge, IA, USA). Once

anesthetized, wolves were weighed, measured, and fitted with the same Acc.-GPS

collars used during behavioral calibration with captive wolves. By selecting free-

ranging adult male wolves, our regional and pack reproductive status comparisons

were not confounded by sex or age-related variation in space use. Our selection also

maximized the likelihood of recording hunting behavior (Mech & Peterson 2003) and

finding kills via GPS clusters during routine monitoring flights (Mech 2012) since

hunting success peaks in 3-5 year old wolves (Sand *et al.* 2006), and male wolves of

this age tend to be the most effective hunters (MacNulty *et al.* 2009).

To address seasonal patterns of movement and energy expenditure, we parsed

the March-October collar deployment window into spring, summer, and fall seasons

based on breakpoints defined by the breeding cycle of wolves in interior Alaska

(Borg *et al.* 2015). Spring (February to April) is the breeding season for Denali

wolves, as females typically enter estrus in March (Mech *et al.* 1998) and, if mated,

have a 2 month gestation period before giving birth to pups in early May (Hayssen &

van Tienhoven 1993). Pup provisioning and rearing is the primary summer (May-

July) activity for packs that have successfully denned and birthed pups (Packard 2003), and individual pack members often hunt independently during this time, carrying food back to the female and her pups (Murie 1944; Haber 1977; Mech 1988). Surviving pups continue to grow and recruit into the pack in the fall (August-October), after which winter (November-January) sets in, and packs resume more cohesive, nomadic patrolling of their territory (Mech *et al.* 1998; Mech & Boitani 2003b).

Hourly GPS data were remotely downloaded from each collar every 3 hours via the Iridium satellite network. Data from these 5 Acc.-GPS collared male wolves was complemented by spatial data from an additional 14 adult wolves (GPS data only; 6 male, 9 female) concurrently monitored as part of a long-term wolf study in DNPP initiated in 1986 (Mech *et al.* 1998; Meier & Burch 2009). During our 8 month study window, data from 13 aerial monitoring flights (Table S4.3) were collected to document current wolf locations and prey remains of recent kills, numbers of pack members, pack composition, active den site locations and use, breeding status of individual wolves, and the timing and suspected causes of mortality. In our analyses, we excluded data from one collared individual traveling independently of any pack (a 'satellite'), one wolf that dispersed out of the study area, and from one pack whose remote western territory precluded frequent aerial pack monitoring.

Analyses

For all Acc.-GPS equipped wolves, we determined energetics by correlating

overall dynamic body acceleration (ODBA), smoothed over a 2 second running mean

(Wilson *et al.* 2006; Shepard *et al.* 2008a), to laboratory-derived rates of oxygen

consumption ($\dot{V}O_2$; e.g. Williams *et al.* 2014). We utilized two different methods to

correlate wolf body acceleration to energetic costs. For our first method, we used

equivalent speeds to link the ODBA values we measured from captive wolves to

published energy expenditures of wolves moving along a range of speeds on a

treadmill (Taylor *et al.* 1982; Weibel *et al.* 1983). Mass-specific metabolic rate

increased with running speed according to

$$\dot{V}O_2 = 0.23 \cdot \text{speed} + 0.13 \qquad (r^2 = 0.79, \, n = 36, \, p < 0.001) \qquad \text{(Eqn. 4.1)}$$

where $\dot{V}O_2$ is in ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ and speed is in $m \cdot s^{-1}$ (Taylor *et al.* 1982). As with

previous studies in terrestrial species (e.g. Halsey *et al.* 2009; Williams *et al.* 2014),

metabolic rate increased linearly as a function of ODBA, according to

$$\text{ODBA} = 0.33 \cdot \text{speed} + 0.29 \quad (r^2 = 0.82, \, n = 17, \, p < 0.001) \qquad \text{(Eqn. 4.2)}$$

where ODBA is in units of gravity (g) and speed is in $m \cdot s^{-1}$. Given the significant

positive linear relationships of both these equations, we combined them to correlate

$\dot{V}O_2$ with ODBA directly according to

$$\dot{V}O_2 = 34.4 \cdot \text{ODBA} + 3.14 \quad (r^2 = 0.83, \, n = 16, \, p < 0.001) \qquad \text{(Eqn. 4.3)}$$

where $\dot{V}O_2$ is in ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ and ODBA is in units of gravity (g).

For our second method, we simultaneously measured ODBA and $\dot{V}O_2$ from

northern breed dogs trained to walk and run within a metabolic chamber on a

treadmill. These "sled dogs" served as trainable proxies for wolves since they are among the oldest domesticated breeds, are of comparable in mass to wolves, and bear the greatest morphological and genomic resemblance to their wild progenitor (reviewed in Bryce & Williams 2017). Similar to Eqn. 4.3, metabolic rate in northern breed dogs increased linearly with body acceleration according to

$$\dot{V}O_2 = 12.01 \cdot ODBA + 6.33 \quad (r^2 = 0.74, n = 25, p < 0.001) \qquad \text{(Eqn. 4.4)}$$

where $\dot{V}O_2$ is in ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ and ODBA is in units of gravity (g).

For both methods, $\dot{V}O_2$ values were smoothed a using 1 minute moving average to represent a physiologically appropriate time scales for changes in metabolic rate (Williams et al. 2014), then converted to kilojoules (kJ) using an energy conversion of 20.1 J per ml O_2, assuming a negligible contribution from anaerobic glycolysis (Taylor *et al.* 1982; Schmidt-Nielsen 1997). Both of the methods described above approximate, rather than directly measure, wolf energetics from collar-derived acceleration data. We are now empirically deriving the wolf ODBA - $\dot{V}O_2$ relationship from captive adult wolves moving at the full range of natural speeds on a treadmill, but data collection was not completed at the time of this dissertation submission. For the remainder of this paper, we present Denali wolf energetic results developed using our first method (e.g. Eqn. 4.3), but present a comparison of results derived from the second method (Fig. S4.2).

We estimated the daily and seasonal per capita minimum daily energy requirements of these wolves by dividing our measured wolf DEE values by 16.8 $J \cdot g^{-1}$ of dry matter (Nagy, Girard & Brown 1999) to calculate daily dry matter needed to

sustain each animal. We then divided this value by 3.33 to account for the fact that consumed animal tissue is ~70% water (i.e. only 30% dry matter, Nagy *et al.* 1999). We multiplied by 1.35 to account for fact that wolves consume approximately 65% of total prey mass from large prey, with the remaining 35% being inedible and/or lost to scavengers (Jedrzejewski *et al.* 2002; Peterson & Ciucci 2003; Wilmers *et al.* 2003; Kaczensky, Hayes & Promberger 2005). Finally, we divided this product by the mass of each wolf to calculate mass-specific energy requirements per kg of tissue for each individual.

To put our results in an ecological context, we made regional comparisons of wolf pack size, home range (i.e. territory) size, and density across the northern extent of DNPP. Pack size was defined as the average of maximum counts observed during all aerial surveys from March-October 2015, and included pups if the pack denned successfully. Wolf packs were recorded as having successfully reproduced if pups were detected during aerial tracking flights (Table S4.3) during the denning season (April through mid-August). Using data from two breeder male Acc.-GPS collared wolves whose packs denned successfully in 2015, we analyzed whether the duration of time spent at the den and the time spent away from the den foraging changed over the course of the summer pup-rearing and recruitment seasons (early May – late August). Following Adams *et al.* (2010), we used within-pack wolf densities (pack size/home range size) rather than regional densities because the number of packs in each region was small enough to bias density estimates (fewer than six packs; Burch *et al.* 2005). In addition, within-pack densities reflect population-wide wolf density

estimates across North American studies (Fuller, Mech & Cochrane 2003; Adams *et al.* 2010).

DNPP landscape attributes and wolf relocation data were integrated and analyzed using the geographic information system ArcGIS (v.10.3.1, ESRI 2015, Redlands, CA). Home ranges for each wolf were calculated using local convex hull (LoCoH) home range estimation, where the 95% isopleth constituted the home range boundary (Getz *et al.* 2007; Downs *et al.* 2012; Fig. S4.3). We then aggregated all fixes from wolves of the same pack to obtain pack LoCoH home range estimates for regional comparisons of habitat use and prey availability. Individual wolves and packs were categorized into each DNPP region described by Adams *et al.* (2010) based on the location of the pack centroid and $\geq 70\%$ of relocations in relation to regional boundaries (Fig. 4.2).

To estimate daily distance traveled (km·day^{-1}) by every collared wolf, we first downsampled each wolf's collar data to 2 fixes/day to account for sampling bias (differences in GPS sample rate across wolves ranged from 2-24 fixes/day) and permit direct comparisons across all wolf spatial datasets. Because daily travel distance estimated from twice-daily GPS fixes undoubtedly underestimates the actual distance traveled by each wolf, we also measured daily travel distance from the five Acc.-GPS equipped wolves (hourly relocations) wolves for comparison. We then used the difference between rarified 2x-daily and 24x-daily GPS fixes from these individuals to re-estimate daily travel distance from the remaining wolves with lower

sampling intervals. Average wolf speed (km·hr^{-1}) on the landscape was estimated from the difference in subsequent GPS locations divided by the sampling interval.

Behavioral classification modeling was conducted using SAS (v.9.3, SAS Institute Inc., Cary, NC, USA), Igor Pro (v.6.37, WaveMetrics, Inc, Lake Oswego, OR, USA), and R (v.3.1.1; R Core Team 2014). Statistical analyses and figures were produced using JMP Pro13 (SAS Institute) and R. All model combinations were fitted with best model fits based on the lowest Akaike information criteria corrected for small sample size (AICc), and study results were expressed as the mean ± s.e.m. (α = 0.05, a priori). Regional, seasonal, and individual-level differences in wolf activity patterns, daily travel distances, and DEE were determined by one way analysis of variance followed by Tukey-Kramer honest significant difference tests. We used least square linear regression to correlate wolf ODBA with speed and energy expenditure, as well as to test for trends in the duration of 1) den site attendance, and 2) foraging bout across the pup-rearing season from Acc.-GPS collared wolves in packs that denned successfully. For all linear models, we checked the assumptions of linearity, normality, and homoscedasticity by visual inspection of plotted residuals.

Results

Behavioral & energetic calibrations

We documented 2904 discrete 2-second captive wolf behavioral observations and corresponding acceleration signatures to train two RF behavioral classification models (mobility and behavioral) using a random subset of these observations (Tables

4.1, S4.1). The training dataset's mobility model segregated wolf behaviors into active and resting periods with high (89%) overall model accuracy, precision, recall, and F-measure (Tables 4.1, S4.4), supporting its validity and application for classifying activity in wild wolves. In our more detailed behavioral model, sleeping was classified correctly most often (96%), eating was classified correctly least often (60%), and resting, locomotor, and other active behaviors had intermediate classification scores (Table 4.1). Overall, behavioral model performance was high (86-96% accuracy for each behavior; Table S4.4).

Field deployment

From March to October 2015, five DNPP adult male wolves were instrumented with Acc.-GPS collars that recorded hourly GPS fixes and continuous tri-axial acceleration for a total of 892 Acc.-GPS wolf days (Table 4.2). Over the course of the 8 month deployment, hourly GPS fixes from these Acc.-GPS collars had a mean (± s.e.m.) fix success rate of 99.7% (±0.08%) and mean time-to-fix interval of 29 seconds (± 1.3 s), allowing for unbiased analyses of resource utilization (Frair *et al.* 2004). An additional 14 DNPP wolves were concurrently monitored via GPS collars which sampled their location 2-8 times daily, depending on configuration, for a total of 3035 GPS-only wolf days (Table 4.2). Because efforts were made to maintain collars on two or more individuals in each pack ranging mostly within DNPP boundaries (Meier & Burch 2009), the 19 total wolves in the present analysis

95

accounted for approximately 40% of the total 2015 DNPP wolf population and provided full spatial coverage of each known pack for the duration of the study.

DNPP has considerable regional and seasonal variation in prey available to wolves. In general, wolf habitat quality, as defined by prey availability, increases from west to east in the DNPP study area (Adams *et al.* 2010). Wolves occupying habitat that supports salmon but few large ungulates (western region) had the lowest within-pack wolf densities (4.7 wolves·1000 km^{-2}) and the smallest average pack size (2.7 wolves·pack^{-1} in 3 packs) relative to regions with more abundant ungulate prey and topographic complexity (central region: 4.8 wolves·1000 km^{-2} and 6.6 wolves·pack^{-1} in 4 packs; eastern region: 8.4 wolves·1000 km^{-2} and 5.3 wolves·pack^{-1} in 2 packs; Table 4.3, Fig. 4.4a,c). On average, the eastern region has supported higher wolf densities for the last 30 years of monitoring ($F_{2,176} = 52.4$, $P < 0.001$; Fig. 4.4d). The mean territory size for wolves in eastern DNPP (845 km^2) was also smaller than that of wolves in the western (1477 km^2) and central (1491 km^2) regions (Fig. 4.4b).

Ungulate densities, estimated in 2015 from fixed-wing aerial and distance-sampling surveys, were approximately 2100 moose, 1750 Dall sheep (primarily in the eastern region), and 2800 caribou in the Denali Caribou Herd (B. Borg, and P. Owen, DNPP, *pers. communication*). The proportion of the Denali Caribou Herd available to each Acc.-GPS wolf was calculated at four times during the study window (mid-March, mid-June, late July, and late September) based on range overlaps between wolves and simultaneously radio collared caribou (L.G. Adams, USGS Alaska

Science Center, *pers. Communication,* Fig. 4.5). The Denali Caribou Herd was mostly located in the central region during the winter and spring, moved into higher country (including larger portions of the eastern region) in the summer, then back down to the central region in the fall. Relative regional availability of other large prey (moose and Dall sheep) was assumed to be seasonally constant. Expressed in moose equivalents (1 moose equivalent = 1 moose, 3 caribou, or 6 sheep) as defined by Fuller (1989) and Keith (1983), these abundances were comparable to previously published estimates of approximately 70 moose equivalents$\cdot$1000 km^{-2} in the western region, and 320 moose equivalents$\cdot$1000 km^{-2} across the central and eastern regions (Adams *et al.* 2010; Rattenbury 2011; Adams 2015; P. Owen, DNPP.

Activity & movement patterns

On average, accelerometer-equipped wolves were active for approximately 40.2 ± 2.7% of each day across the study window (33-47% range, Fig. 4.6a). Depending on the individual, wolves were walking or running for approximately 1% to 10% of each day, with the remaining ≥30% of active behaviors comprised of interacting, grooming, eating, and other non-locomotor activities (Table S4.1, Fig. 4.6b). Season had no effect on the proportion of time spent active each day (37-41% range, $F_{2, 10} = 0.27$, $p = 0.77$; Fig. 4.6c) and similarly, seasonal variation was not detected for any of the 5 behaviors in the more detailed behavioral RF model (p range = 0.19-0.83; Fig. 4.6d).

According to GPS-derived movement rates, wolves traveled, on average, faster during summer ($\bar{x} = 0.92 \pm 0.02$ km·h^{-1}) than fall ($\bar{x} = 0.78 \pm 0.02$ km·h^{-1}) and spring ($\bar{x} = 0.65 \pm 0.02$ km·h^{-1}, $F_{2, 20,664} = 69.2$, $p < 0.001$). When grouped by region from March-October, movement rates were highest for eastern wolves ($\bar{x} = 0.93 \pm 0.02$ km·h^{-1}), followed by those occurring in western ($\bar{x} = 0.85 \pm 0.01$ km·h^{-1}) and central ($\bar{x} = 0.61 \pm 0.01$ km·h^{-1}, $F_{2, 20,664} = 91.5$, $p < 0.01$ for each comparison) regions of DNPP. In spring and summer, movement rates of Acc.-GPS individuals in packs that successfully reproduced in 2015 did not differ from those of wolves in packs that failed to reproduce (p range = 0.16-0.7). During pup recruitment in the fall, however, adult males in packs with young pups traveled slower ($\bar{x} = 0.72 \pm 0.02$ km·h^{-1}) than their pup-free conspecifics ($\bar{x} = 0.98 \pm 0.03$ km·h^{-1}, $t (6353) = 48.9$, $p < 0.001$).

Daily wolf travel distance (km·d^{-1}; Table 4.3, Fig. 4.7) averaged 1.59x farther (range: 1.47-1.82) when derived from hourly fixes of Acc.-GPS collared wolves, compared to downsampled (twice-daily) estimates from these same individuals. We therefore used this value as a correction factor to estimate hourly travel distance from wolf collars with less frequent spatial sampling. Wolves in western DNPP traveled significantly shorter distances during the breeding season (15.6 ± 0.8 km·d^{-1}) compared to the pup-rearing and recruitment seasons (18.3 ± 0.7 and 18.0 ± 0.8 km·d^{-1} respectively, $F_{2, 998} = 3.7$, $p = 0.03$). Daily distance traveled did not vary with reproductive season for wolves in eastern DNPP ($F_{2, 723} = 2.2$, $p = 0.12$), where individuals averaged 17.4 km·d^{-1} (16.6-18.3 km·d^{-1}, 95% CI) throughout the study window. In contrast, central DNPP wolves showed distinct seasonal fluctuations in

daily travel distance, with the longest movements occurring during the May-July pup-rearing season ($\bar{x}$ = 24.6 km·d^{-1}, compared with 16.5 km·d^{-1} and 20.8 km·d^{-1} during breeding and recruitment seasons, respectively; $F_{2, 954}$= 17.8, p < 0.001). These farther average summer routes by central DNPP wolves were also significantly longer than travel paths taken by conspecifics to the west or east (p < 0.03).

Energetic costs

DEE pooled across all accelerometer-equipped wolves for the duration of our study averaged 17,404 ± 208 kJ·wolf^{-1} (Table 4.4). After accounting for mammalian carnivore digestive efficiency and water mass in consumed animal tissues, this expenditure equates to a wolf per capita daily food requirement of 3.45 kg of prey. In the regional comparison across seasons, average DEE was significantly lower for wolves in central DNPP (14,117 ± 360 kJ·day^{-1}) than those to the west (19,042 ± 286 kJ·day^{-1}) or east ($\bar{x}$ = 18,264 ± 404 kJ·wolf^{-1}; $F_{2, 891}$ = 60.4, p < 0.001). These daily demands varied seasonally in DNPP ($F_{2, 891}$ = 16.5, p < 0.001), with costs averaging 15,633, 18,445, and 17,711 kJ for adult male wolves in spring, summer, and fall, respectively (Table 4.4, Fig. 4.8). DEE was lowest during the spring, although costs were higher for western wolves (1502M and 1506M) than conspecifics elsewhere in the Park ($F_{2, 258}$ = 21.6, p < 0.001). Daily costs among wolves did not vary regionally over the summer ($F_{3, 362}$ = 1.9, p = 0.15), but did again in the fall ($F_{2, 265}$ = 73.6, p < 0.001). Western wolves had the highest recorded DEE measurements in both spring (41,127 kJ·day^{-1}) and summer (38,020 kJ·day^{-1}), whereas maximum fall DEE was

slightly higher in the eastern Acc.-GPS wolf we monitored (38,132 kJ·day^{-1} *vs.* 36,907 kJ·day^{-1} in eastern and western wolves, respectively).

Patterns of hourly energy expenditure varied among wolves as well, with some individuals exhibiting crepuscular activity at dawn and dusk (e.g. Bearpaw pack wolf 1506M) and others showing more diurnal activity (e.g. Myrtle pack wolf 1503M; Fig. 4.9). The mean hourly costs associated with these activity patterns was lower for wolves in central DNPP ($\bar{x} = 560.2 \pm 19.9$ kJ·h^{-1}) compared to those to the west ($\bar{x} = 758.6 \pm 19.9$ kJ·h^{-1}) or east ($\bar{x} = 760.6 \pm 28.7$ kJ·h^{-1}, $F_{3, 121} = 29.9$, $p < 0.001$; Fig. 4.10), but this was likely influenced by the truncated dataset from wolf 1507M that was shot 50 days into the study.

Using these DEEs, we estimated the minimum number of moose, caribou, or Dall sheep required by packs with Acc.-GPS collared wolves at seasonal, deployment-wide, and annual timescales (Table 4.5). Assuming a dynamic equilibrium in which energy gains meet or exceed energy losses, wolf prey demands peaked during the pup-rearing summer months to meet seasonally elevated DEE (Tables 4.4, 4.5). Furthermore, we estimated that an average pack of 5 wolves would need to annually consume a minimum of approximately 33 moose, 74 caribou, or 189 Dall sheep (or some combination) to pay off its 6112.6 MJ metabolic debt and balance the energy budget (Table 4.5).

Reproductive success

The pooled March-October DEE of wolves in packs that successfully

reproduced and raised pups in 2015 (17,359 ± 234 kJ· wolf^{-1}) did not differ from

those that did not raise a litter (17,516 ± 430 kJ·wolf^{-1}; t (427) = -0.32, p = 0.75).

However, we noted distinctions after accounting for seasons. In the spring breeding

season, males in packs that gave birth to pups expended, on average, more energy

than those in packs that were reproductively unsuccessful ($\bar{x}$ = 16,695 ± 484 vs.

14,081 ± 549 kJ· wolf^{-1}, respectively; t (235) = 3.6, p < 0.001). These energetic

differences disappeared during the summer months (t (136) = -0.7, p = 0.46)), and

were reversed in the fall ($\bar{x}$ = 16,587 ± 419 *vs.* 21,085 ± 854 kJ· wolf^{-1} for wolves in

reproductively successful and non-successful packs, respectively; t (100) = -4.7, p <

0.001).

As predicted on the basis of habitat quality, wolf pack reproductive success in

2015 increased from west to east in DNPP (Table 4.5). In the western flats, only 33%

of packs (1 of 3) birthed and raised pups. In contrast, 50% of packs (2 of 4) in the

central region successfully reared pups, and both (100%) of the eastern packs gave

birth to and recruited pups into their packs. For the three Acc.-GPS collared wolves in

reproductively successful packs (Bearpaw, Myrtle, and Grant Creek), the amount of

time spent at the den did not change predictably over the course of the pup-rearing

season. However, we noted contrasting trends in foraging bout length (hours away

from the den) with the duration into the pup-rearing season in these three packs (Fig.

S4.4). Over the course of the denning season, foraging bouts became shorter for

wolves in western and eastern regions (from approx. 40 hrs to 10 hrs, $p = 0.049$ and from 40 hrs to 20 hrs, $p = 0.03$, respectively), but lengthened for Acc.-GPS equipped central wolf we monitored (from approx. 10 hrs to 60 hrs; $p < 0.003$).

Discussion

We captured instantaneous- to seasonal-timescale variations in behavior and DEE from adult male wolves outfitted with accelerometer-GPS collars to infer how prey availability and pup-rearing might impact the movement ecology of these wide-ranging carnivores. Our results demonstrate that the underlying activity patterns of Denali wolves, as measured by the metabolic demands of free-ranging behavior, vary markedly with season, pack reproductive status, and habitat heterogeneity across the study area. For example, wolves in the western flats had overall higher mean and maximum DEE than central or eastern DNPP wolves (Table 4.4, Fig. 4.7). Wolves in western DNPP are thought to have limited access to large ungulates and therefore derive up to one third of their diet from Pacific salmon (Adams *et al.* 2010; Fig. 4.3). Generally, wolves there occur in smaller packs and at lower densities than in habitats to the east, which are more topographically complex and host more abundant (and diverse) ungulate prey (Fig 4.4a,c). Historical data from 30 years of wolf monitoring confirm this trend of low wolf density in the western flats despite lower human harvest of wolves there, suggesting that this is lower quality wolf habitat (Fig. 4.4d).

Nevertheless, certain territories within western DNPP may be suitable to support relatively large wolf packs, as exemplified by wolf 1502M and his mate

1006F in the Bearpaw pack, which successfully reared 6 pups in 2015. 1502M foraged for shorter and shorter periods as the pup-rearing season wore on. This may be due to an increased demand to remain at the den to look after the large litter, an ephemeral surge of accessible prey (e.g. summer-run Chinook or chum salmon in the nearby Otter Creek), or some unknown cause. In contrast, the Myrtle pack (1503M and his mate 1504F) produced 3 pups in the relatively prey-replete central region, and the breeder male's time away from the den (presumably hunting to provision for the nursing female and pups) significantly increased as the pups grew. The divergent patterns of wolf foraging bout duration throughout the pup-rearing season may be the result of differential prey availability or provisioning demands on the breeder males of these packs.

Our 8-month comparison of reproductively successful *vs*. unsuccessful breeder males revealed no significant differences and had several important limitations. First, our limited sample size constrained our ability to replicate matched pairs of successful *vs*. unsuccessful breeder males while controlling for known regional variation in habitat and prey across DNPP. Second, one of our Acc.-GPS collared individuals, 1507M, was legally harvested near the Park boundary just 50 days into the March – October study, precluding our ability to track his reproductive success and activity patterns in comparison to the other Acc.-GPS wolf in central DNPP, 1503M. Lastly, we cannot definitively attribute energetic differences to breeding status because differences in energetics and breeding status could both be due to local prey availability for each pack. Additional studies, where prey abundance

is constant, are needed to more conclusively compare net energy balance (acquisition

minus loss) with reproductive output in breeder wolves.

For highly mobile animals like wolves, habitat structure and metabolic

transport costs are inextricably linked. Heterogeneity in the external environment

(including incline, vegetation, and substrate type) influences animal movement costs

(e.g. Fancy & White 1987; Wilson, Quintana & Hobson 2012; Shepard *et al.* 2013),

and in turn these movement costs impact how animals move through and interact with

their environment (e.g. Halsey 2016; Scharf *et al.* 2016). DNPP wolf home ranges

encompassing mountainous terrain in the Alaska Range underscore the impact of the

surrounding environment on modulating transit costs. Wolves in the Grant Creek

pack, for example, routinely traversed high alpine passes (>2000 m) while traveling

from their den site (south of the Range) to preferred hunting grounds (north of the

Range) and back. Judicious use of energy stores (e.g. via least-cost route selection),

may be critical for heavy animals like wolves, which experience higher absolute and

relative net transport costs for uphill locomotion and less downhill 'reimbursement'

than lighter animals (Halsey & White 2017; but see Reichman & Aitchinson 1981).

As with other animals, wolf movement ecology is driven by seasonally-

variable internal state and external factors (reviewed in Nathan *et al.* 2008).

Ecological travel costs include the energy expenditure associated with turning,

intermittent locomotion, and kinematic responses to the surrounding environment

(Kramer & McLaughlin 2001; Bidder *et al.* 2012a; Wilson *et al.* 2013a). The

ecological cost of travel for a 23-kg wolf was estimated to be 16% of DEE (Steudel

2000), and this proportion would be higher for gray wolves in DNPP that are twice as heavy. Similarly, the accelerometer-equipped wolves we monitored were highly mobile (Table 4.3, Fig. 4.7) and active for roughly 40% or 10 hours of each day (Fig. 4.6), comparable to previous estimates (e.g. Theuerkauf *et al.* 2003; Eggermann *et al.* 2009).

Additional spatial data from 14 concurrently GPS-monitored wolves in DNPP helped elucidate regional and seasonal activity patterns from Acc.-GPS wolves. We found that the average daily travel distance remained roughly constant throughout the study window only for wolves in eastern DNPP (Fig. 4.7). Contrary to our prediction, we found no evidence that wolves in western DNPP reduce their daily travel distance (Fig. 4.7) or DEE (Fig. 4.8) during fall (Table 4.4), when spawning Pacific-run salmon are available and may constitute a substantial proportion of the diet for wolves in this region (Adams *et al.* 2010). Furthermore, travel distance and DEE for western wolves increased for each consecutively monitored season (Table 4.4), implying that local access to salmon may not be driving the movement patterns we observed. The interior Alaska salmon run undergoes high inter-annual variability and in 2015, for example, the total Yukon River run of fall chum salmon was well below the forecast (i.e. lower than average for an odd-numbered year) and was attributed to poor age-4 production from the primary parent year (B. Borba, ADFG, *pers. communication*). Similarly, fall 2015 coho salmon escapement estimates in the region were lower than long term averages (Estensen, Borba & Gleason 2015), suggesting that salmon may have provided only a marginal nutrient subsidy to wolves that year.

Travel patterns were highly variable across seasons for wolves in central DNPP. Daily displacement and DEE peaked during in summer months for these wolves, which moved, on average, 7 km·d^{-1} farther than conspecifics to the east or west (Tables 3,4, Fig. 4.7). One potential driver of these farther summer travel bouts is the seasonal change in the migratory distribution of the Denali Caribou Herd (Adams & Roffler 2010). As the herd migrates from low-elevation winter ranges to the summer calving ranges in the foothills to the N-NW of Mt. Denali to forage and escape insect pests, the percent of the Herd available to wolves in the central region declines (Fig. 4.5). As a result, locating and pursuing increasingly scare caribou in the summer may contribute to greater proportions of time spent traveling and higher energy expenditure for wolves there (Table 4.4, Fig. 4.8). Wolves in eastern DNPP experience greater caribou availability in summer, but after the caribou rut in late September, these prey migrate once again through central DNPP wolf territories (Fig. 4.5), becoming a more readily available fall and winter prey base for wolves there.

Across individuals and seasons, the average daily energy requirement we measured from wild adult male wolves ($\bar{x}$ = 17,460 ± 248 kJ·wolf·d^{-1}; 12,619-21,043 kJ·wolf·d^{-1} range; Table 4.4) is comparable to the previous FMR reported for wolves ($\bar{x}$ = 17,700 kJ·d^{-1} from 6 timber wolves in northern Minnesota; Swain, Costa, and Mech, cited in Nagy 1994, 1999). Other estimates of daily energy requirements for wolves range from 21,300 kJ to 25,025 kJ per wolf (Glowacinski & Profus 1997; Kreeger 2003; Peterson & Ciucci 2003). The daily energy requirements we derived may be slightly lower than previous estimates due to methodological or study system

differences. Rather than measuring FMR over several days using DLW or estimating

it with a multiple of BMR, we used equivalent travel speeds to link mass-specific

wolf oxygen consumption measurements (Taylor *et al.* 1982) to collar-derived ODBA

values from wild conspecifics. In addition, previous estimates of wolf energy

requirements were from 35-40 kg wolves preying on deer in mixed temperate forest

and agricultural lands, whereas DNPP wolves are 10+ kg heavier, occupy boreal and

alpine habitats, and consume larger ungulates. Despite these differences, the per

capita minimum energy requirement we estimated for wolves is 3.46 kg of prey per

day, or 0.074 kg prey per kg wolf per day. Our estimate falls within the range of

reported daily food requirements for wolves (0.06 to 0.29 kg prey per kg wolf), as

estimated from 18 North American studies (summarized in Peterson & Ciucci 2003).

Indeed, energy requirements for wolves are approximately 25% higher than a typical

eutherian mammal of similar body mass, suggesting that wolves must consume

considerably more than would be expected based on their body mass (Nagy *et al.*

1999).

How, therefore, do wolves meet these elevated demands for prey?

Researchers have hypothesized that sociality (here, group hunting) in wolves and

other large carnivores facilitates their ability to subdue larger prey and ultimately

increase per capita consumption (e.g. Gittleman 1989; Post *et al.* 1999). Numerous

studies, however, have shown that hunting success and food availability per wolf

declines as pack size increases beyond 2-4 individuals (Thurber & Peterson 1993;

Schmidt & Mech 1997; Hayes & Harestad 2000; MacNulty *et al.* 2011; Mech *et al.*

2015; but see Jedrzejewski *et al.* 2002), although when hunting bison, success

increases across larger pack sizes (MacNulty *et al.* 2014). The advantage of wolf

sociality and group hunting, however, may come through minimizing carcass loss to

scavengers (Vucetich, Peterson & Waite 2004; Kaczensky *et al.* 2005), thereby

enabling breeding pairs to provision their offspring the short term food surplus from

group-hunted kill (Schmidt & Mech 1997; Mech & Boitani 2003b).

The cumulative costs associated with wolf sociality (e.g. sharing kills,

interacting) and cursorial hunting mode drive these high kill rates in wolves (Miquelle

et al. 2005). Despite long travel and chase distances, low hunting success rates further

exacerbate the costs of predation (Mech *et al.* 2015a). Across large ungulate prey

species found in Denali (moose, caribou, and Dall sheep), wolf hunting success

averaged only 15% based on the number of individual prey animals over 8 studies,

and 35% over 5 studies based on the number of hunts (i.e. encounters involving prey;

summarized in Mech & Peterson 2003).

Our analyses focused solely on quantifying wild wolf activity patterns and

energy expenditure (rather than energy intake via prey consumption as well) in part

due to the remoteness of the field site. The snow-free study period, coupled with the

outlying locations of DNPP pack territories, precluded our ability to field-verify wolf

kill remains from GPS clusters. However, field studies capable of investigating even a

small number of GPS clusters stand to benefit from using accelerometry in

combination with GPS telemetry to estimate kill rate (and therefore energy intake) for

wolves. For example, GPS fixes associated with field-validated wolf-kills can be

matched with the corresponding accelerometer record post-hoc. This enables investigators to filter for an accelerometer signature associated with the kill and even each phase of the hunt (Williams *et al.* 2014), which have been described in detail for wolves (e.g. MacNulty, Mech & Smith 2007). Using a classification approach such as the RF we present here, one could analyze immense accelerometer datasets for probable kills of each prey species of interest, since wolves utilize unique hunting strategies for different prey (Mech *et al.* 2015a). Once an accelerometer signature library is assembled for successful kills of each prey type, this approach may prove critical for estimating kill rate in study areas like Denali, where field-verifying GPS clusters if logistically challenging or cost prohibitive.

Because energy demand ultimately motivates an animal's behavioral decisions, our study demonstrates the capacity of integrating GPS and accelerometry to reveal activity and energetic insights from wide-ranging predators in unprecedented detail. Given that DNPP is a relatively undisturbed ecosystem, wolf travel patterns and resource requirements there may represent the baseline needs for wolves occurring elsewhere. As northern latitudes continue to rapidly warm and change (e.g. Post *et al.* 2009), knowing this baseline becomes necessary for tracking how fluctuations in snowfall patterns, plant phenology and growth, etc. cascade up to impact the abundance and distribution herbivores, as well as the predators that rely on them (Estes *et al.* 2011; Ripple *et al.* 2014). In lower latitudes, currently recovering gray wolf populations in the United States are being delisted from the Endangered Species Act of 1973 (Tollefson 2013). As these populations lose federal protection,

insight into wolf foraging patterns and prey requirements obtained via Acc.-GPS

telemetry may be invaluable for informing regionally specific management decisions

and promoting the persistence of this keystone species throughout its range.

Table 4.1: Random forest model confusion matrix of training data showing the number of 2-second observations classified into the mobility model (resting *vs.* active) and the behavior model (5 behaviors). The number and % of correct classifications for each behavior are denoted in bold.

Mobility model

	Rest	Active
Rest	**3177 (93%)**	417
Eat	257	**2931 (88%)**

Behavior model

	Rest	Walk & Run	Eat	Active	Sleep
Rest	**1253 (73%)**	89	55	184	50
Walk & Run	123	**668 (69%)**	21	328	4
Eat	79	39	**164 (60%)**	20	1
Active	131	164	28	**1400 (71%)**	11
Sleep	121	12	6	33	**1791 (96%)**

Table 4.2: Summary and regional distribution of wolves monitored in Denali National Park and Preserve from March-October, 2015. M and F designate collared male and female wolves, respectively; regional totals are denoted in bold.

| Region | Pack | Reprod.? | Max. Pup Count | Pack Size | GPS | | Acc.-GPS | |
					GPS-only Wolves	Days Monitored	Acc.-GPS Wolf ID	Days Monitored
West	Bearpaw	Yes	6	2 to 8	1F	242	1502M	212
West	Hot Slough	No		1 to 2	1F, 1M	291		
West	John Hansen	No		2 to 5	1M	241	1506M	209
West	**3 packs**	**1 of 3**	**Up to 6**	**Up to 8**	**4**	**774**	**2**	**421**
Central	East Fork	No		1 to 14	1F, 1M	243	1507M	50
Central	Iron Creek West	Yes	6	2 to 15	1F, 1M	476		
Central	McKinley Slough	No		2	1F, 1M	481		
Central	Myrtle	Yes	3	2 to 7	1F	229	1503M	210
Central	**4 packs**	**2 of 4**	**Up to 6**	**Up to 15**	**7**	**935**	**2**	**260**
East	Grant Creek	Yes	7	2 to 9	1F	241	1501M	211
East	Riley Creek	Yes	5	2 to 9	1F, 1M	485		
East	**2 packs**	**2 of 2**	**Up to 7**	**Up to 9**	**3**	**726**	**1**	**211**
Total	**9 packs**	**5 of 9**	**Up to 7**	**Up to 15**	**14**	**3,035**	**5**	**892**

112

Table 4.3: Regional comparison of mean (± s.e.m.) DNPP wolf pack size, home range size, within-pack density, and daily travel distance from 19 wolves in 9 packs during March-October, 2015. Wolf counts represent the maximum observed, including pups, in each region during the study window.

| Region | Area (km^2) | Packs, wolves | Pack size | Home range (km^2) | Wolf density* | Daily travel distance (km) | | | |
						Spring	Summer	Fall	March-Oct.
Western	7127	3, 15	2.7 ± 0.7	1478 ± 901	4.7 ± 3.4	15.6[i,A] ± 0.8	18.3[i,A] ± 0.7	18.0[i,A] ± 0.8	17.4[a] ± 0.5
Central	5048	4, 38	6.6 ± 2.4	1491 ± 345	4.8 ± 1.7	16.5[i,A] ± 1.0	24.6[ii,B] ± 0.9	20.8[iii,A] ± 1.0	20.8[b] ± 0.5
Eastern	2786	2, 18	5.3 ± 0.6	845 ± 389	8.4 ± 4.5	16.0[i,A] ± 1.1	16.8[i,A] ± 1.0	18.9[i-iii,A] ± 1.0	17.3[a] ± 0.6

* Within-pack wolf density, expressed as the number of wolves per 1000 km^2

[i-iii] Within-region seasonal means comparisons not sharing a common Roman numeral differ significantly ($p < 0.05$).

[A,B] Among-region seasonal means comparisons not sharing a common uppercase letter differ significantly ($p < 0.05$).

[a,b] Among-region March-October means comparisons not sharing a common uppercase letter differ significantly ($p < 0.05$).

Table 4.4: Seasonal and deployment-wide mean (± s.e.m.) daily distance traveled (km·d⁻¹) and daily energy expenditure (DEE in kJ·d⁻¹, in bold) for Acc.-GPS equipped wolves in Denali National Park and Preserve. Daily distance traveled was calculated from hourly relocations from each instrumented individual.

Wolf	Mass (kg)	Pack	Region	Reprod.?	Daily estimate by season			Daily estimate (Mar-Oct. pooled)
					Spring	Summer	Fall	
1502M	48	Bearpaw	West	Yes	$15.0^{i,a} \pm 0.6$	$18.6^{i,a} \pm 1.1$	$18.8^{i,a} \pm 1.0$	$17.8^{A} \pm 0.6$
					$20923^{i,a} \pm 916$	**$18792^{i,a} \pm 582$**	**$18750^{i,a} \pm 536$**	**$19311^{A} \pm 384$**
1506M	51	John Hansen	West	No	$16.8^{i,a} \pm 2.0$	$21.1^{i-ii,a} \pm 1.4$	$23.5^{ii,b} \pm 1.5$	$21.0^{B} \pm 0.9$
					$15629^{i,b} \pm 887$	**$18391^{ii,a} \pm 686$**	**$21085^{ii,b} \pm 854$**	**$18777^{A} \pm 482$**
1507M	45.5	East Fork	Central	No	$13.0^{a} \pm 1.3$	NA	NA	$13.0^{A} \pm 1.3$
					$12591^{c} \pm 597$	**NA**	**NA**	**$12591^{B} \pm 597$**
1503M	43	Myrtle	Central	Yes	$13.9^{i,a} \pm 0.8$	$20.3^{ii,a} \pm 1.2$	$7.7^{iii,c} \pm 0.7$	$14.7^{A} \pm 0.8$
					$13894^{i,b-c} \pm 539$	**$17414^{ii,a} \pm 593$**	**$10989^{iii,c} \pm 342$**	**$14509^{B} \pm 364$**
1501M	46	Grant Creek	East	Yes	$17.4^{i,a} \pm 2.0$	$23.6^{ii,a} \pm 1.4$	$23.9^{ii,b} \pm 1.5$	$22.1^{B} \pm 0.9$
					$15213^{i,b-c} \pm 668$	**$18710^{ii,a} \pm 582$**	**$20023^{ii,a-b} \pm 684$**	**$18264^{A} \pm 392$**
$\bar{x}$ km·d⁻¹	49.5	Pooled	West		15.9 ± 1.1	20.1 ± 0.9	21.2 ± 0.9	$19.4^{A} \pm 0.6$
$\bar{x}$ **kJ·d⁻¹**					**18276 ± 543**	**19570 ± 535**	**20464 ± 514**	**$19450^{A} \pm 323$**
$\bar{x}$ km·d⁻¹	44.3	"	Central		13.9 ± 1.6	20.3 ± 1.2	7.7 ± 0.7	$14.7^{B} \pm 0.8$
$\bar{x}$ **kJ·d⁻¹**					**13232 ± 538**	**18314 ± 715**	**11107 ± 357**	**$13937^{B} \pm 384$**
$\bar{x}$ km·d⁻¹	46	"	East		17.4 ± 2.0	23.6 ± 1.4	23.9 ± 1.5	$22.1^{A} \pm 0.9$
$\bar{x}$ **kJ·d⁻¹**	"				**15213 ± 668**	**18728 ± 588**	**19945 ± 717**	**$18254^{B} \pm 392$**
$\bar{x}$ km·d⁻¹	46.7 ± 1.3	Pooled	All	3 of 5	$15.3^{a} \pm 0.8$	$20.9^{b} \pm 0.6$	$18.5^{c} \pm 0.7$	18.6 ± 0.4
$\bar{x}$ **kJ·d⁻¹**	"	"	"	"	**$15633^{a} \pm 372$**	**$18445^{b} \pm 309$**	**$17711^{b} \pm 398$**	**17404 ± 208**

[i-iii] Within-wolf seasonal means comparisons not sharing a common Roman numeral differ significantly ($p < 0.05$).

[a-c] Among-wolf seasonal means comparisons not sharing a common lowercase letter differ significantly ($p < 0.05$).

[A-B] Pooled daily km and kJ means comparisons not sharing a common capital letter differ significantly ($p < 0.05$).

Table 4.5: Pack count, per capita DEE (MJ·wolf^{-1}·d^{-1}), and estimated minimum ungulate prey requirements at seasonal, deployment-wide, and annual temporal scales for 5 wolf packs in Denali National Park and Preserve. Pack counts are presented as total wolves, with number of pups in parentheses.

Pack		Seasonal averages			Total req. (March-Oct.)	Total req. (Annual)
		Spring	Summer	Fall		
Bearpaw	Total (pups[A])	2 (0)	8 (6)	8 (2)		
	Avg. MJ·wolf^{-1}·d^{-1}	20.9	19.7	19.4	5467	7309
	Moose[B] req.	3.4	12.9	12.7	29	43.4
	Caribou[B] req.	7.7	28.9	28.5	65.1	97.4
	Dall sheep[B] req.	19.5	73.6	72.5	165.6	247.7
John Hansen	Total (pups)	5 (0)	5 (0)	3 (0)		
	Avg. MJ·wolf^{-1}·d^{-1}	15.6	19.4	21	5104	6828
	Moose req.	6.4	7.9	5.2	19.5	29.2
	Caribou req.	14.3	17.8	11.6	43.7	65.4
	Dall sheep req.	36.4	45.3	29.4	111.1	166.2
East Fork	Total (pups)	14 (0)	3 (0)	4 (0)		
	Avg. MJ·wolf^{-1}·d^{-1}	12.6	12.6C	12.6C	3445	4606
	Moose req.	14.4	3.1	4.1	21.6	32.3
	Caribou req.	32.4	6.9	9.3	48.6	72.7
	Dall sheep req.	82.4	17.7	23.5	123.6	184.9
Myrtle	Total (pups)	2 (0)	5 (3)	6 (4)		
	Avg. MJ·wolf^{-1}·d^{-1}	13.9	18.3	11.1	3937	5264
	Moose req.	2.6	7.5	5.4	15.5	23.2
	Caribou req.	5.1	16.8	12.2	34.1	51
	Dall sheep req.	12.9	42.7	31.1	86.7	129.7
Grant Creek	Total (pups)	4 (0)	7 (3)	6 (2)		
	Avg. MJ·wolf^{-1}·d^{-1}	15.2	18.7	19.9	4904	6556
	Moose req.	5	10.7	9.8	25.5	38.1
	Caribou req.	11.2	24	21.9	57.1	85.4
	Dall sheep req.	28.4	61.1	55.8	145.3	217.4
Averages pooled across packs	**Total (pups)**	**4.8 (0)**	**6 (2.4)**	**5.4 (2)**		
	Avg. MJ·wolf^{-1}·d^{-1}	**15.6**	**19**	**17.9**	**4571.4**	**6112.6**
	Moose req.	**6.4**	**8.4**	**7.4**	**22.2**	**33.2**
	Caribou req.	**14.1**	**18.9**	**16.7**	**49.7**	**74.4**
	Dall sheep req.	**35.9**	**48.1**	**42.5**	**126.5**	**189.2**

[A]Given their mass and the elevated energy demands associated with growth, we assumed that subadult and pup energy requirements were approx. 1/3 of adults.
[B]Prey masses are averaged DNPP adult male and female values: moose (400 kg), caribou (178 kg), and Dall sheep (70 kg).
[C]Due to the premature loss of East Fork wolf 1502M, we estimated prey consumption for the remainder of the pack during our study period by extending 1502M's per capita prey consumption.
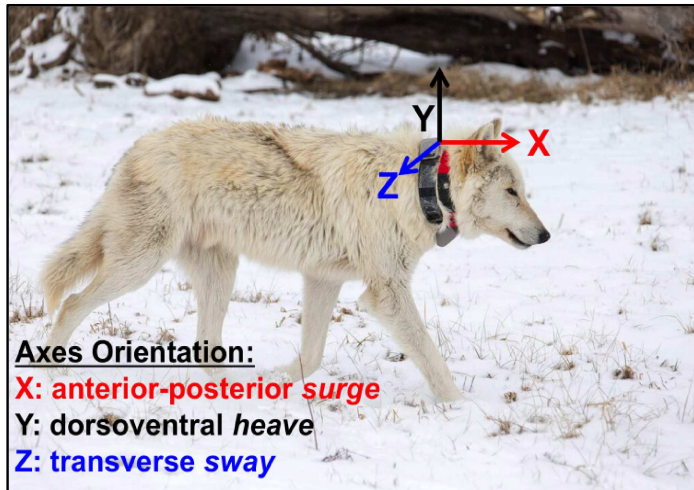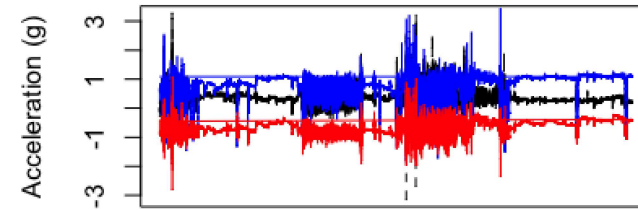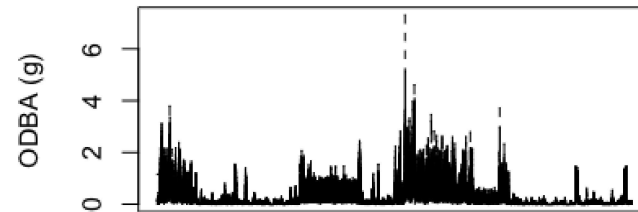
Figure 4.1: Wolf accelerometer-GPS collar calibration, showing axis orientation (A). A 1-hour raw data sample shows how distinct behaviors generate unique collar accelerometer signatures (B) and associated ODBA values (C).
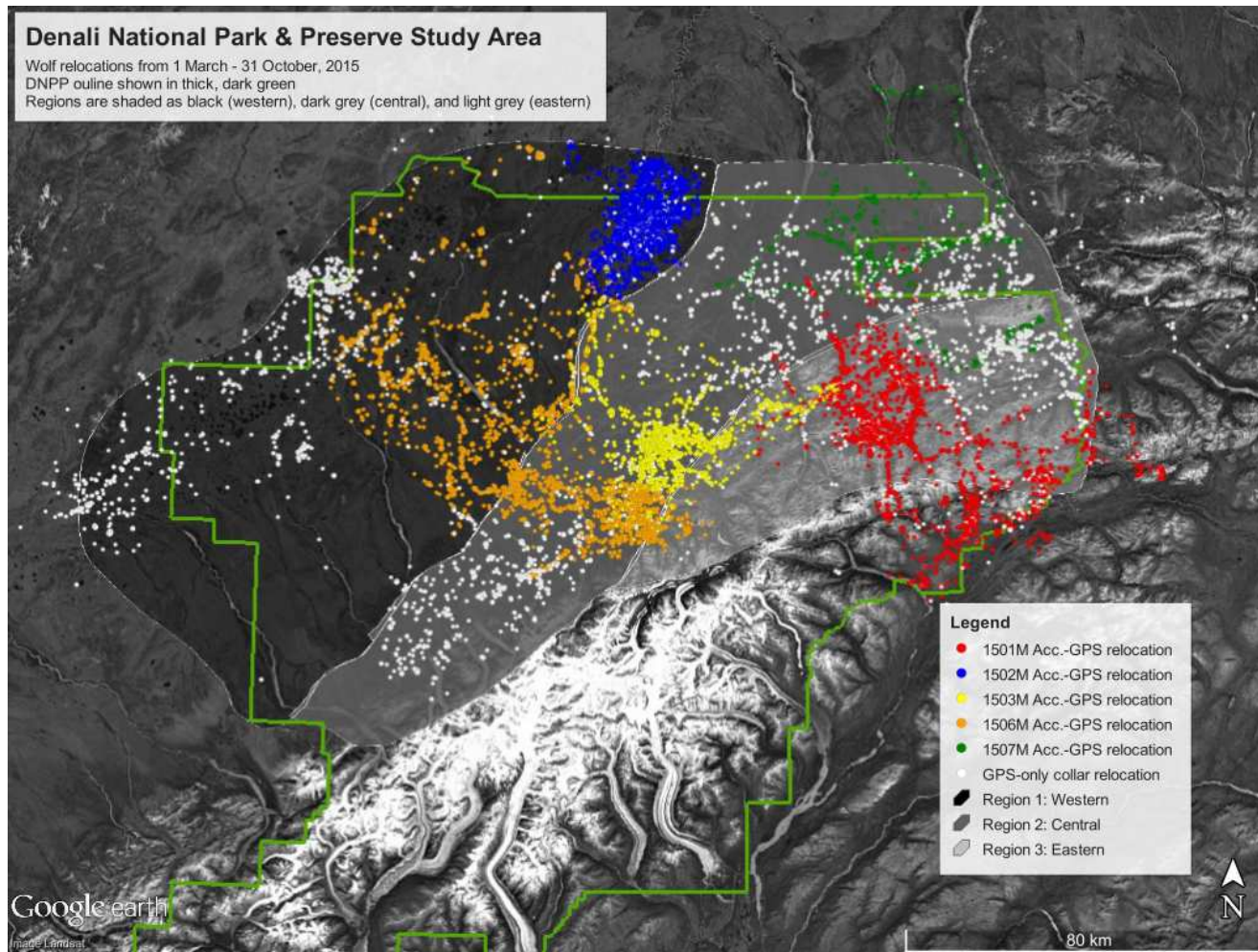
Figure 4.2: Map of DNPP study area north of the Alaska Range crest, showing all wolf relocations used in analyses from 1 March – 31 October 2015. White dots are relocations from 14 GPS-only collared wolves, and colored dots are relocations from 5 Acc.-GPS collared wolves. Regions are demarked by shaded polygons according to Adams et al. (2010).
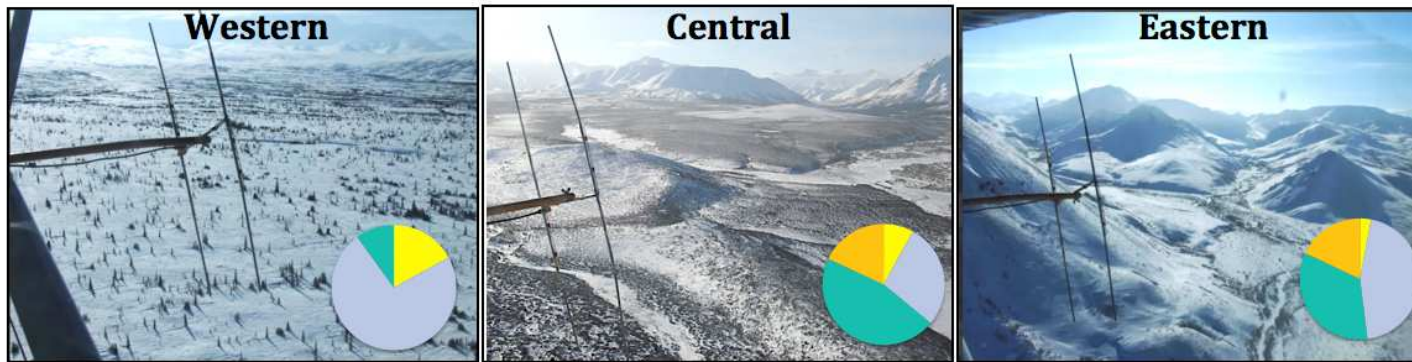
Figure 4.3: Regional variation in both habitat and prey available to wolves in DNPP north of the Alaska Range. From west to east, salmon availability declines but large ungulate prey are more abundant, particularly where Dall sheep are available in the more mountainous eastern region. Colored pie chart insets reflect the estimated proportion of each wolf prey type in each region based on the latest survey data.
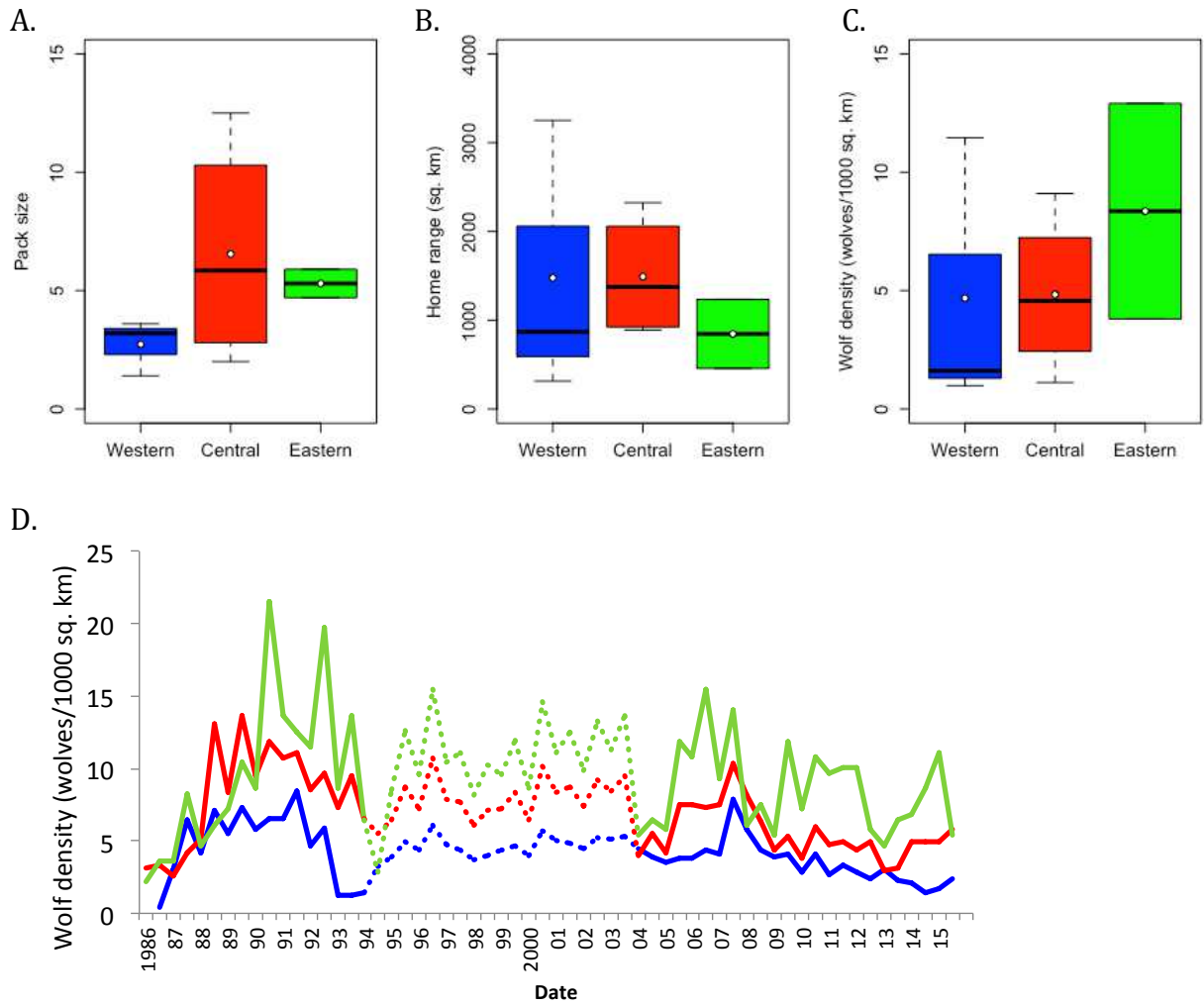
Figure 4.4: Regional variation in mean pack size (A), home range (B), and wolf density (C) from March – October 2015. White dots in box-and-whisker plots are regional means. Thirty years of longitudinal data (D) confirm that, on average, the eastern portion of DNPP supports higher densities of wolves. Densities from 1994-2004 (dotted lines) were unavailable but modeled from long-term trends. Home ranges were smallest for packs in the Eastern region (B), although the average pack size of these wolves was intermediate relative to packs to the west (A).
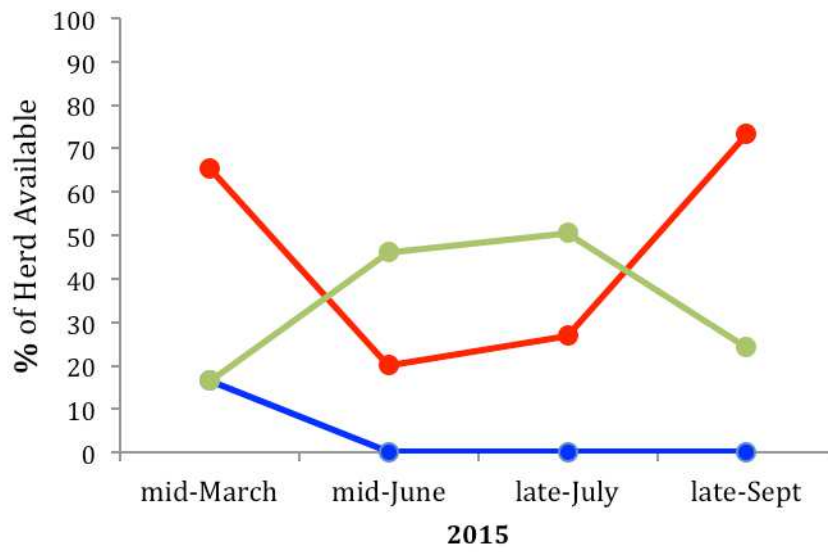
Figure 4.5: Percentage of the Denali Caribou Herd available to Acc.-GPS wolves in the western (blue), central (red) and eastern (green) regions of DNPP.
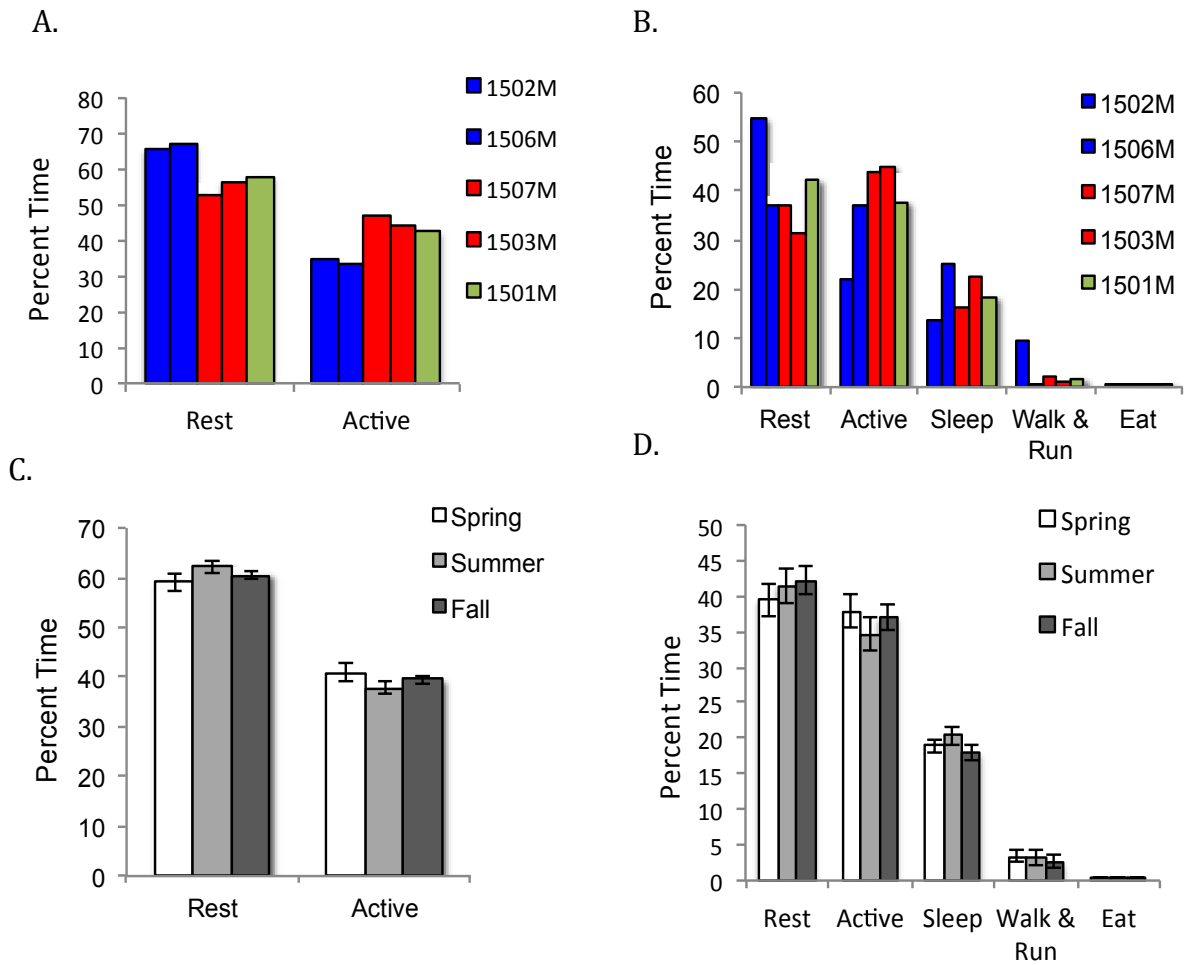
Figure 4.6: Individual (A, B) and seasonal (C, D) daily activity patterns (mean and 95% CI) of 5 adult male wolves in Denali National Park and Preserve from March—October 2015. Colors denote DNPP region (west = blue, central = red, east= green) and season (white = spring, light grey = summer, dark grey = fall) for both the mobility (rest *vs.* active behavior; A, C) and the 5-behavior (B, D) RF models.
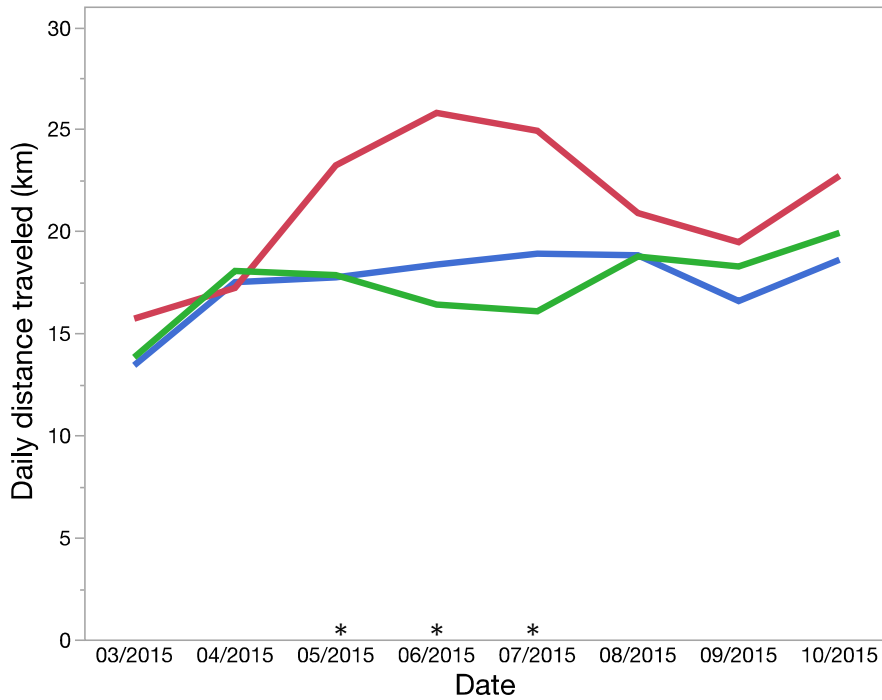
Figure 4.7: **Average daily travel distance (km) by month for wolves in western (blue), central (red), and eastern (green) regions of DNPP in 2015.** Central wolves traveled significantly farther ($F_{2, 954} = 17.8$, $p < 0.001$) than their western and eastern conspecifics during May, June, and July.
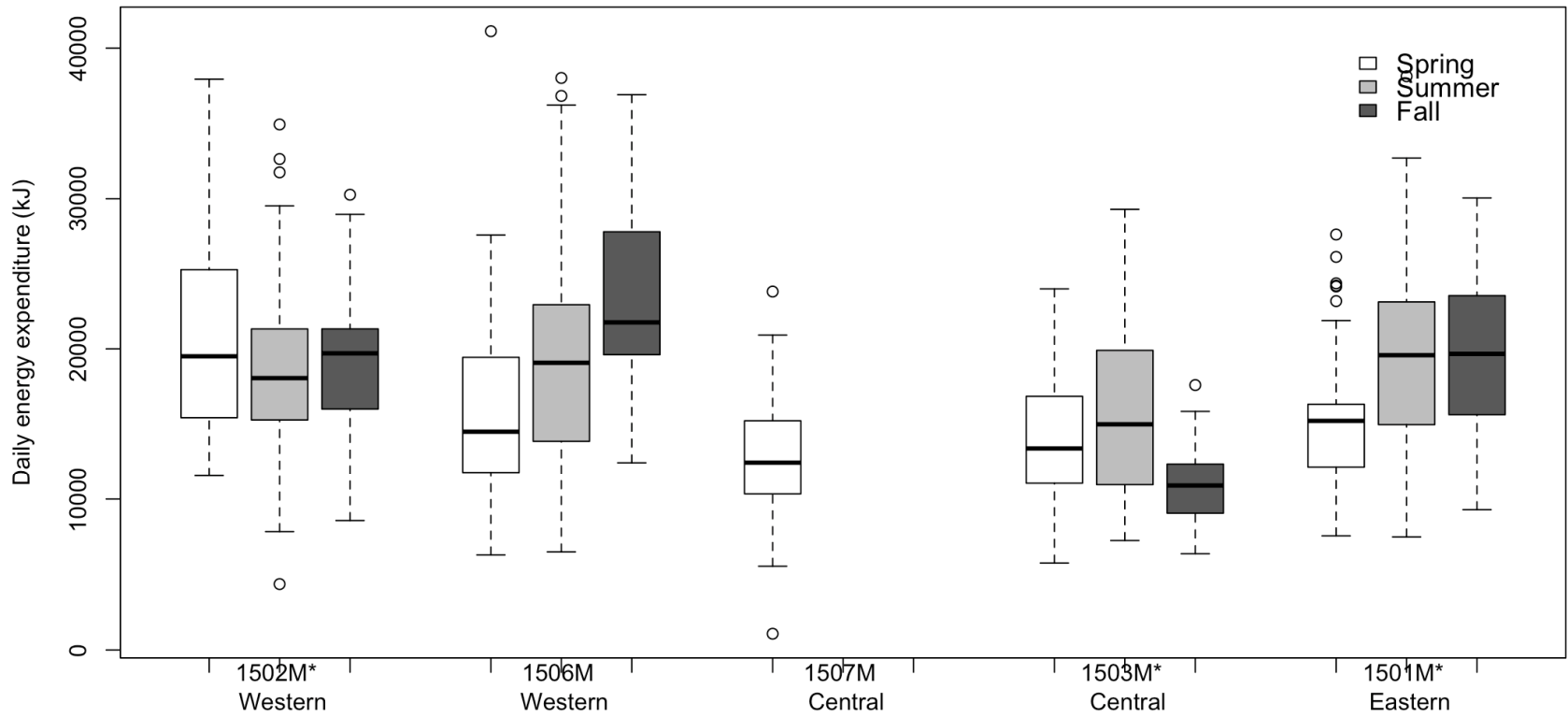
Figure 4.8: Seasonal variation in DEE (kJ) from 5 Acc.-GPS collared wolves across DNPP. Asterisks (*) denote wolves in packs that were reproductively successful in 2015 (Bearpaw, Myrtle, and Grant Creek packs, respectively).

123

A.

Wolf 1502M, Bearpaw pack (western region)

B.

Wolf 1506M, John Hansen pack (western region)

C.

Wolf 1507M, East Fork pack (central region)

D.

Wolf 1503M, Myrtle pack (central region)

E.

Wolf 1501M, Grant Creek pack (eastern region)
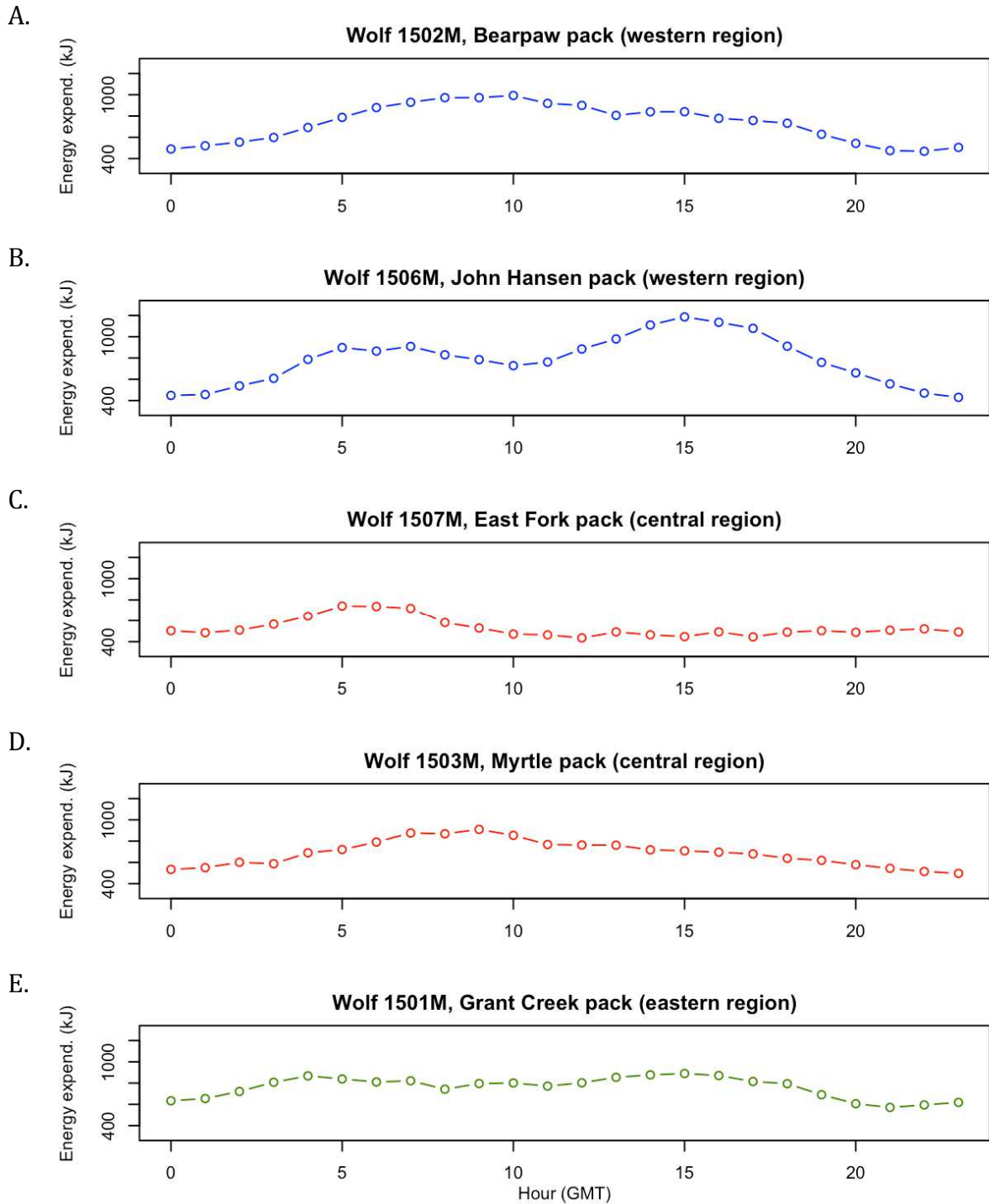
Figure 4.9: Hourly variation in average energy expenditure (kJ·h⁻¹) from 5 Acc.-GPS collared wolves in western (blue, A, B), central (red, C, D), and eastern (green, E) regions of DNPP. Means are presented for hourly energy cost for the entire March -- October study window, except for Wolf 1507M, who was shot 50 days into the study. Note that hour 0 corresponds to midnight.
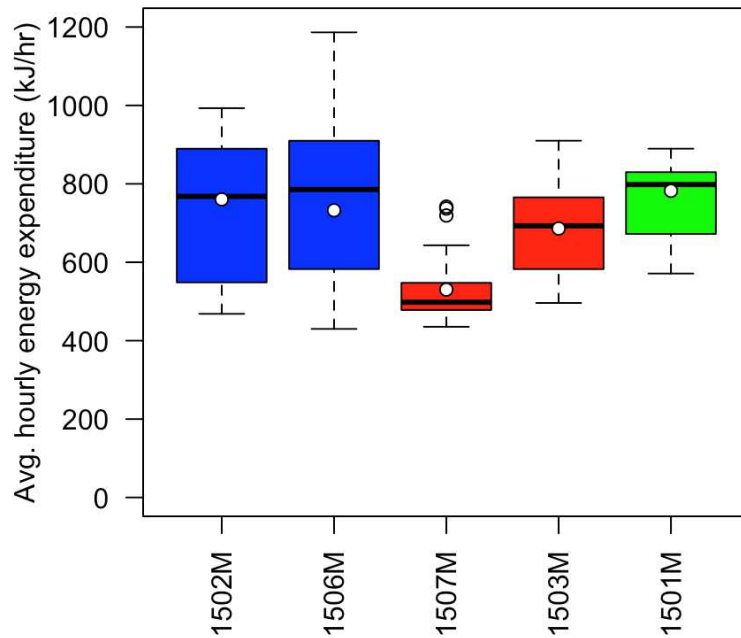
**Figure 4.10: Regional variation in average hourly energy expenditure (kJ·h^{-1})
from 5 Acc.-GPS collared wolves** in western (blue), central (red), and eastern
(green) regions of DNPP. White dots in box-and-whisker plots are means. Hourly
costs for wolves in central DNPP were significantly lower ($p < 0.05$) than for wolves
to the west or east, but this is likely influenced by the shooting of wolf 1507M 50
days into the study.

Table S4.1: Total 2-second observations of captive wolf behaviors used in random forest training datasets for each behavior.

Mobility Model

Behavioral state	Included behaviors	N	% of Total
Rest	Sleep, stand, sit, lie down	1539	53
Active	Locomotion, groom, eat, interact	1365	47

Behavioral Model

Behavior state	Included behaviors	N	% of Total
Rest	Stand, sit, lie down (alert)	698	24.1
Walk & Run	All locomotor gaits (walk, trot, gallop)	489	16.9
Eat	Bite, tear, shred, chew	129	4.4
Active	Interact, groom	743	25.6
Sleep		841	29

Table S4.2: Ten parameters extracted from raw tri-axial accelerometer data to predict wolf behaviors in mobility (active *vs.* resting) and behavioral (5 behaviors) random forest (RF) models.

Parameter	Label	Definition
Static acceleration (g)	sbaX, sbaY, sbaZ, sbaQ	Static acceleration along the surge, heave, sway, and magnitude axes.
Dynamic body acceleration (g)	dynX, dynY, dynZ, dynQ	Dynamic body acceleration along the surge, heave, sway, and magnitude axes.
Overall dynamic body acceleration (g)	odba	odba = odbaX+odbaY+odbaZ; mean dynamic acceleration body acceleration along the surge, heave, and sway axes.
Vectorial dynamic body acceleration (g)	VeDBA	Mean vectorial dynamic body acceleration.

Table S4.3: Aerial DNPP wolf monitoring flight schedule & wolf counts showing pack size and composition (March – October, 2015).

Approx. Date[a]	3/4	3/7	3/19	3/23	3/29	4/29	5/24	7/25	8/2	8/15	9/25	10/9	10/10
Wolf Season[b]	Br	Br	Br	Br	Br	Br	Br	PR	PR	PR	Rec	Rec	Rec
Pack													
Bearpaw	2	NL	2	2	2	LOH	2	2	NR	NV	BP +7p	NC	3 killing moose
Grant Crk*	NL	NL	4	4	4	3	1	1	6p	BP +7p	BP +2p	6	+2p
East Fork	NL	1	13	14	14	6	5	1	NR	3	2 min.	4	NR
Myrtle*	NYD	NYD	2	NL	NL	2	2	BP +3p	NR	3p min.	BP +3p	BP+1a +3p	BP+1a
John Hansen	5	NL	5	5	5	2	2	2	NR	2	3	3	2
Riley Crk*	NL	5	5	5	5	LOH	at den	NV	4p	BP +5p	BP +5p	4a 5p	NR
McKinley Sl.	2	NL	2	2	2	2	2	LONH	NR	NV	2	NR	NR
Iron Crk West*	7	NL	NL	7	NL	2	2	BP+1a +6p	6p	NR	15 6p min.	NR	NR
Hot Slough	2	NL	3	2	NL	2	NR	NR	NR	1	1	1	NR

[a]Monitoring date is approximate and based on date of filed flight narrative
[b]Wolf seasons: Br: breeding; PR: pup raising; Rec: pup recruitment
*denotes pack that was reproductively successful in 2015
Acronyms = a: adults; BP: breeding pair; LOH: listened only, heard (VHF); LONH: listened only, not heard (VHF); min.: minimum; NC: no change from previous report; NL: not located; NYD: not yet discovered; NR: not reported; p: pups

Table S4.4: Performance of the random forest mobility and behavioral models in classifying captive wolf behaviors.

Mobility Model

Behavior	MCC[a]	Accuracy	Precision	Recall	*F*-measure
Rest	0.78	0.89	0.92	0.86	0.89
Active	0.78	0.89	0.92	0.86	0.89

[a] Matthews' Correlation Coefficient; Matthews (1975)

Behavioral Model

Behavior	MCC[a]	Accuracy	Precision	Recall	*F*-measure
Rest	0.68	0.88	0.74	0.79	0.76
Walk & Run	0.54	0.88	0.69	0.54	0.6
Eat	0.59	0.97	0.68	0.53	0.6
Active	0.65	0.86	0.69	0.81	0.75
Sleep	0.9	0.96	0.95	0.91	0.93

[a] Matthews' Correlation Coefficient; Matthews (1975)

A.
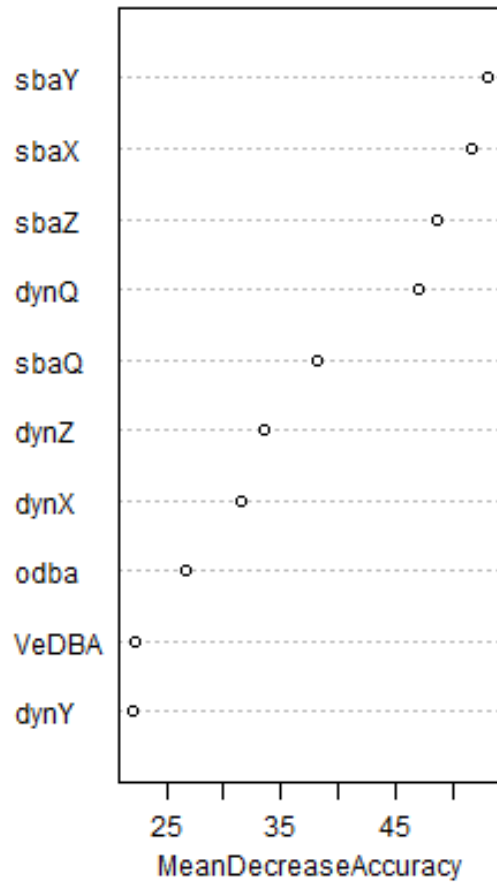
B.
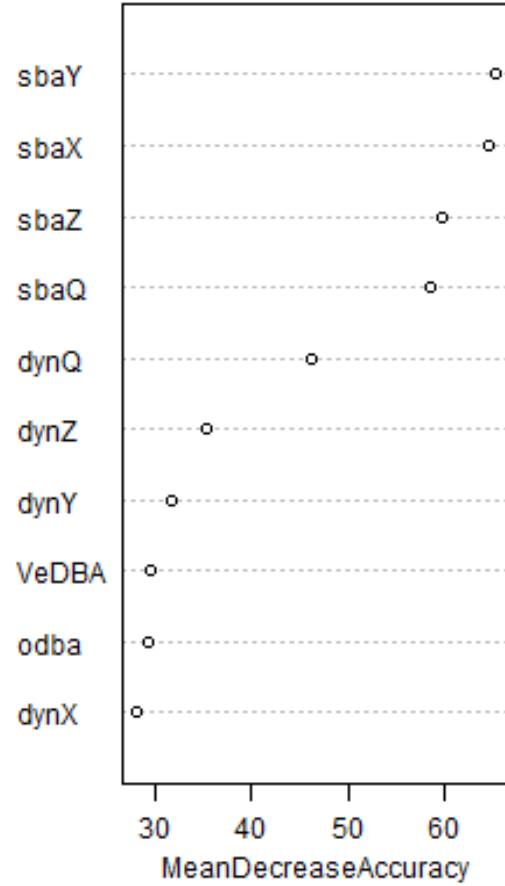
Figure S4.1: Random forest model variable importance plots for mobility (A) and behavioral (B) models. Higher values indicate parameters that contributed more to behavioral classification accuracy. Static acceleration in the Y, X and Z-axes were most important for classification accuracy in both models.
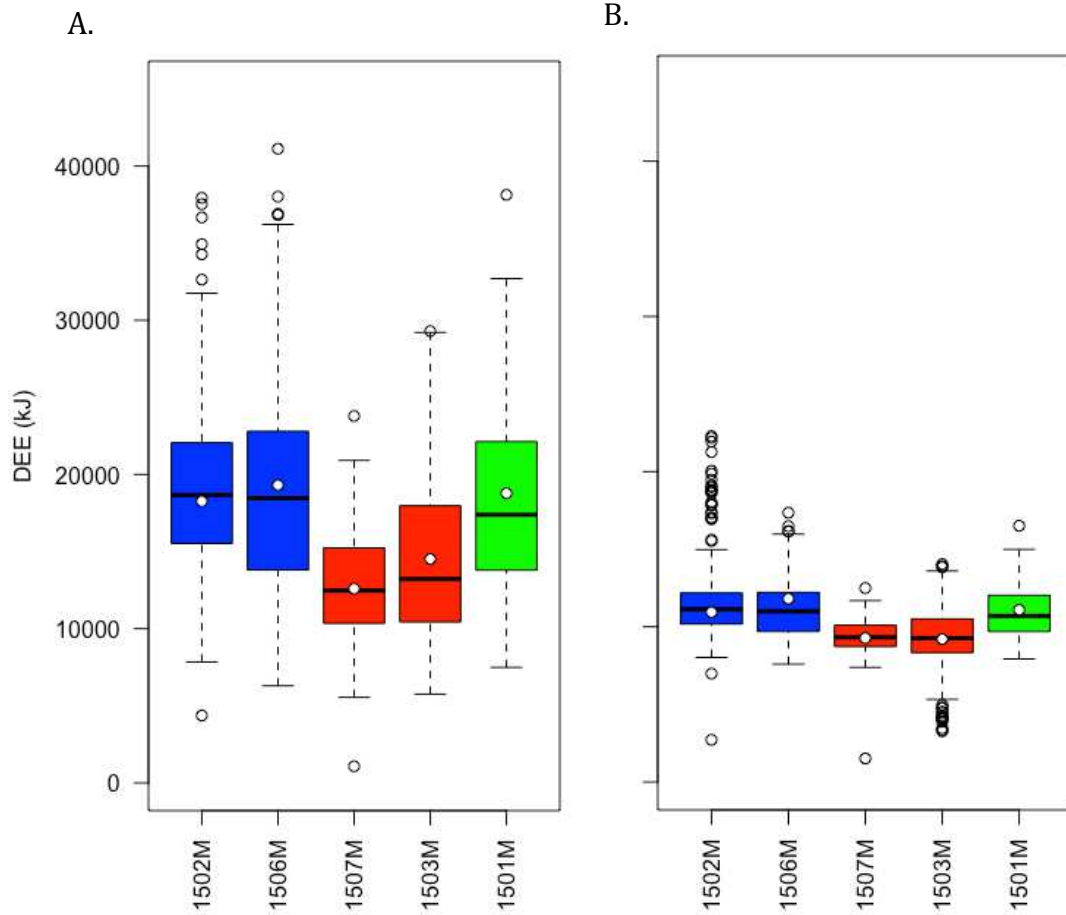
Figure S4.2: Comparison of average wolf daily energy expenditure (DEE in kJ) derived by using the equivalent speed method (A) and the northern breed dog proxy method (B). Data are from 5 Acc.-GPS collared wolves in western (blue), central (red), and eastern (green) regions of DNPP. White dots in box-and-whisker plots are means.
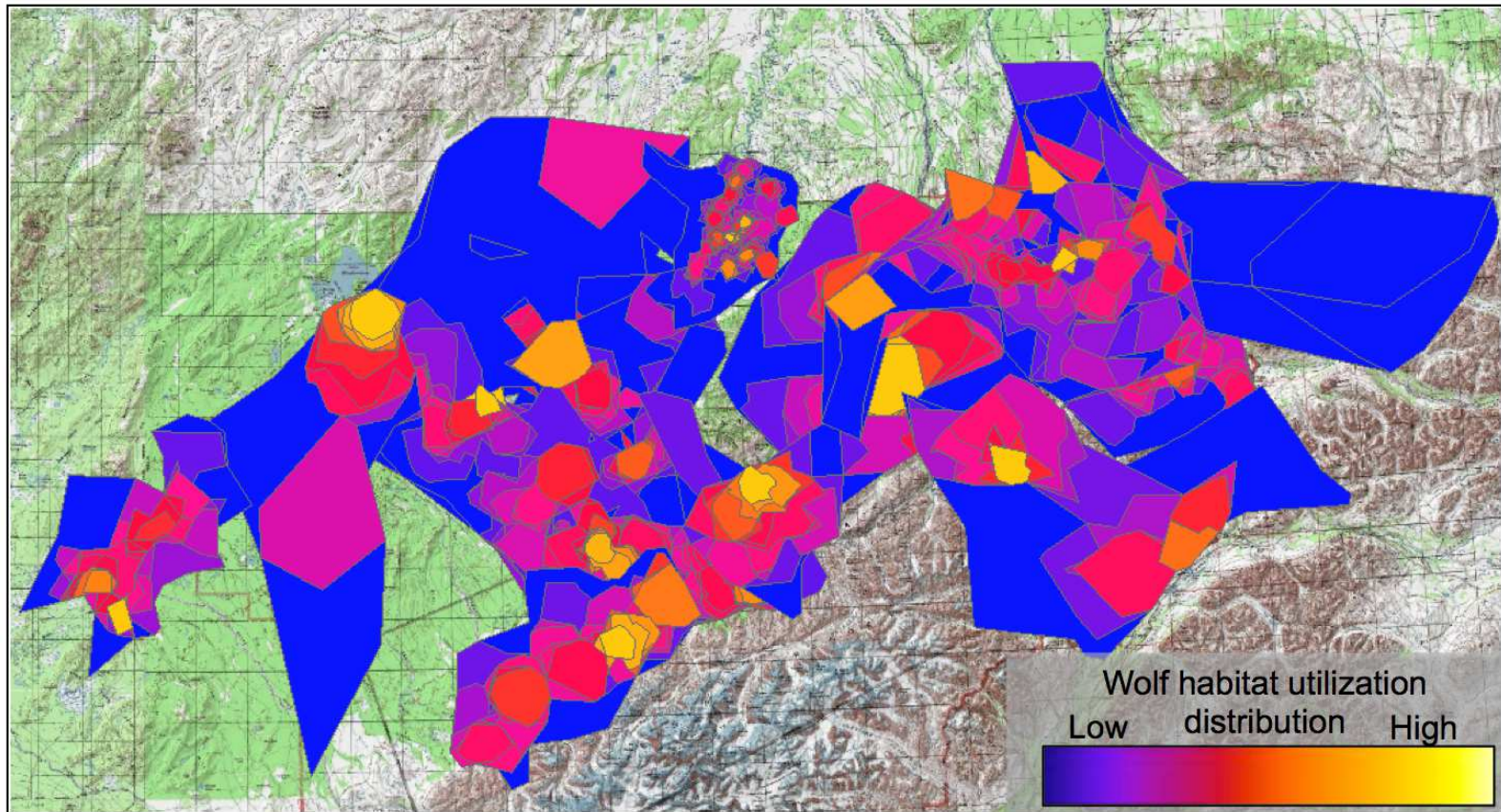
Figure S4.3: Habitat utilization based on Localized Convex Hull (LoCoH) home range estimation from 19 wolves in Denali National Park and Preserve, March – October, 2015. Individual isopleth polygons depict regions of low (cool colors) to high (warm colors) habitat use based on telemetry data at 5% home range intervals.
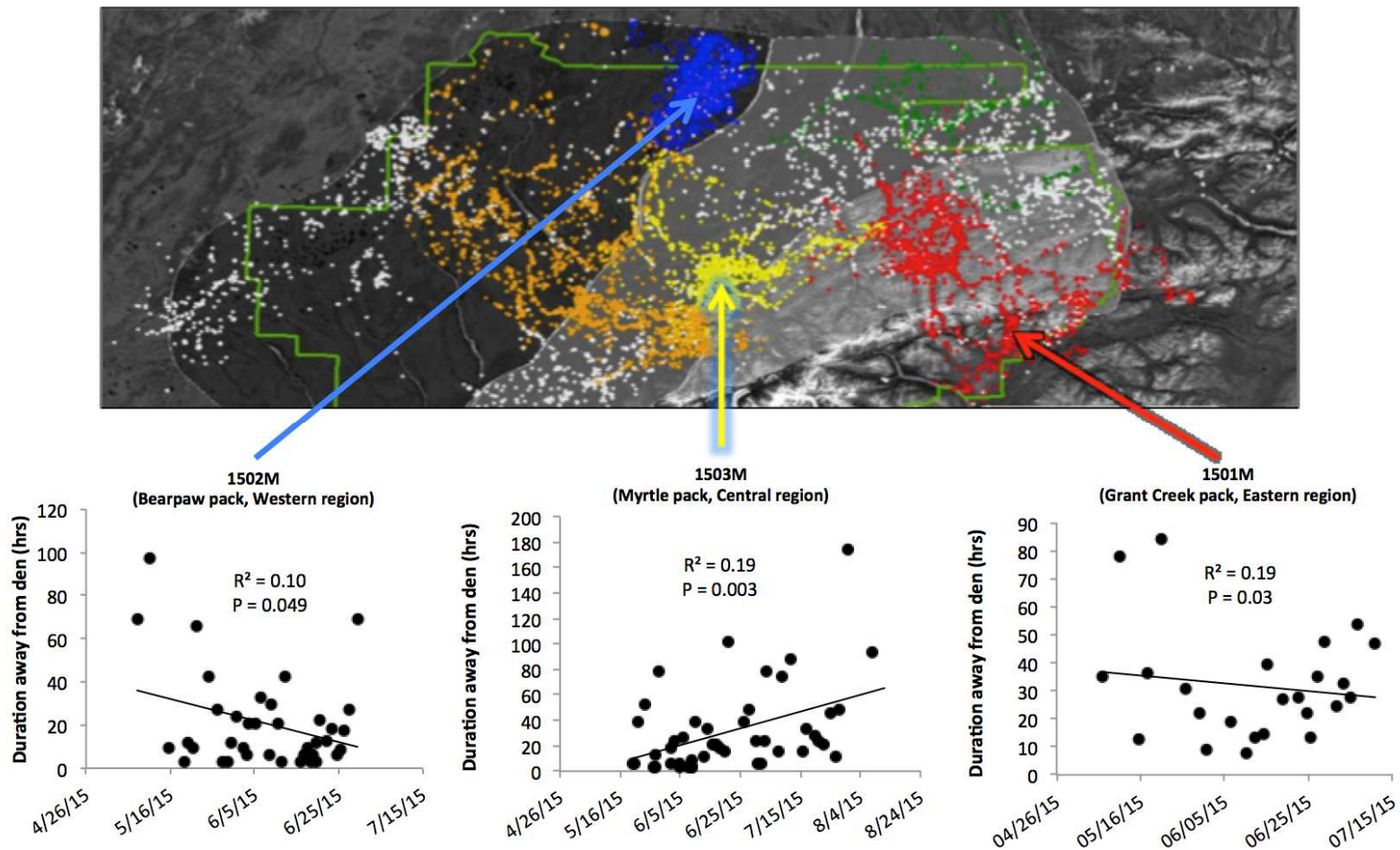
Figure S4.4: Wolf foraging bout length (hours away from den) as a function of duration into the pup-rearing season for 3 Acc.-GPS collared wolves in DNPP. Breeder male wolves in western and eastern Denali spent less time away from the den site as the pups grew (A, C), but the Acc.-GPS collared male in central Denali (B) spent more time afield as the summer wore on, presumably to hunt increasingly scarce migratory caribou in the region.

CHAPTER 5

Synthesis

Integrating physiology into large carnivore research and management

In the Forward of a recent treatise exploring physiological mechanisms and evolutionary necessities in the adaptation of mammals (Withers *et al.* 2016b), Brian K. McNab writes, "A physiological approach to the behavior and ecology of organisms is fundamental to our understanding of the characteristics required of species for survival… [This approach] is uniquely capable of examining the mechanistic basis of the responses of species to the environment." Furthermore, understanding animal metabolic energy demand is of fundamental importance to a variety of scientists and practitioners. Physiologists seek to understand how animals have adapted to particular environments; ecologists interpret the diverse roles organisms play in their ecosystems; and managers are interested in how species' resource requirements inform strategic conservation planning.

Integrating physiology into our ecological understanding of large carnivores ought to remain a research priority because energy demand ultimately determines the behavioral decisions these predators make, driving where and how often they feed

(Stephens & Krebs 1986; Speakman 2000; Brown et al. 2004; Humphries & McCann 2014). In turn, these predation rates and wide-ranging movement patterns impact the ability of large carnivores to structure vast ecosystems through cascading trophic effects, whether density or behaviorally-mediated (Terborgh & Estes 2010; Ripple *et al.* 2014).

As highly cursorial group-hunting predators, large canids exemplify the capability of physiological constraints (e.g. elevated metabolic rates) to impact community-wide dynamics in nature. Wolves require substantial prey and supporting habitat, yet deliver economic and ecosystem services via both direct and indirect pathways (reviewed in Ripple *et al.* 2014). Furthermore, wolves have diverse and documented effects on mesopredator dynamics (Ripple *et al.* 2013), scavenger subsidies (Wilmers *et al.* 2003), disease dynamics (Wilmers *et al.* 2006), stream morphology (Beschta & Ripple 2012), and even carbon cycling (Wilmers & Schmitz 2016). In light of these complex interactions and ecosystem-scale effects, quantifying the activities and energetic demands of wolves and other mobile carnivores is crucial for effective management by elucidating resource requirements (Berger-Tal *et al.* 2011; Laundré 2014), but has remained exceedingly difficult.

This dissertation, in part, has field-validated innovative technology for monitoring wild carnivores, including wolves and pumas. Alongside a dedicated team of computer engineers, wildlife ecologists, and animal trainers, I helped to develop accelerometer-GPS collars (Rutishauser *et al.* 2011; Williams *et al.* 2014) calibrated for wild canids and felids, together with the analytical tools for data interpretation.

Using a similar approach, scientists and resource managers alike are now equipped to examine the mechanistic basis of how large, free-living carnivores respond to changes in their surrounding environment. Continued use and further development of animal-borne sensors is critical to understanding the nuanced interplay of physiology, behavior, the environment, and climate (Kays et al. 2015; Wilmers et al. 2015; Williams, Barnes & Buck 2016). Thus, identifying fine-scale behavioral and movement patterns in these species represents a critical step towards evaluating how both prey densities and natural and anthropogenic landscape features influence predator space use and energy allocation.

Conservation implications

The global importance of both terrestrial and marine apex predators in ecosystem structure and persistence cannot be overstated. In their edited volume on predators, prey, and the changing dynamics of nature (Terborgh & Estes 2010), distinguished ecologists James A. Estes and John Terborgh provide a solemn reminder: "Of all the trophic layers we have lost or are losing, the top carnivore layer is the most crucial to the survival of contemporary nature, because the top down regulation it provides stabilizes the interactions between consumers and producers."

In an increasingly human-dominated world, the long-term survival of large terrestrial carnivores such as pumas and wolves depends on finding ways for people to coexist with them. The large carnivore guild includes some world's most iconic animals, yet ironically some of the most imperiled. From human intolerance and

direct persecution to more insidious effects such as habitat fragmentation, large

carnivores today face a worldwide barrage of threats (Estes *et al.* 2011; Ripple *et al.*

2014). Indeed, over one quarter of the carnivorous mammals are now globally

threatened or already extinct in the wild (Schipper *et al.* 2008; IUCN 2016).

The far-ranging movements of these predators necessitate our need to

maintain viable populations outside of parks and reserves, as few protected

landscapes are large enough to ensure their long-term persistence at ecologically

functional densities (Lande 1988; Oriol-cotterill *et al.* 2015). This is especially

relevant in the continental United States, where wolves, black bears, and pumas are

each now recolonizing much of their historic range and, as a result, coming into

increased conflict with humans and livestock (LaRue *et al.* 2012; Smith, Nielsen &

Hellgren 2015a; Bangs 2016; U.S. Fish & Wildlife Service 2016). Novel technology

and analytical approaches like those presented in this dissertation can be utilized to

confront these management challenges. Data obtained from animal-borne sensors can

reveal how landscape-scale changes in the environment affect the physiological

demands of predators and so influence their survival, reproduction, ecological impact,

and conflict with humans (Wilmers *et al.* 2015).

Future directions

To facilitate widespread adoption of this approach and maximize its

conservation potential, we have already delivered this technology to a wildlife collar

manufacturing company (Vectronics Aerospace, Berlin, Germany), which has made it available worldwide. In addition, the programmatic code written for collar data analysis (e.g., classifying wolf behavior, modeling energy use on the landscape) will be made available upon publication of project results. As presented in this dissertation, data derived from such animal-borne technology can enhance our understanding of the links between wild carnivore habitats, prey thresholds, and movement patterns. Together, these parameters are critical for projecting the future abundance and distribution of large carnivores in increasingly altered landscapes.

Fortunately, the laboratory-to-field approach and animal-borne technology described here are already gaining traction within the wildlife management and conservation communities. Researchers and managers eager to deploy our collar for their own projects have already been approaching our team. To date, these include long-term carnivore monitoring efforts throughout North America: in the Greater Yellowstone Ecosystem, the Canadian Rockies, and Ellesmere Island in the Arctic Circle. If you include ongoing collaborative projects within our team (studying the African carnivore guild, tropical dolphins and seals, sea otters, and polar-living whales, bears, and seals), the applications of ecophysiological approaches like those described in this dissertation are truly global.

Going forward, I intend to continue conducting meaningful physiological ecology research while having a measurable impact on conservation policy, management, and outreach in the broader community. My work with large carnivores has underscored the value yet vulnerability of these animals in the ecosystems they

inhabit, and I believe I have the responsibility to conduct quality research that generates pertinent, management-oriented data on these and other animals and threatened habitats. Given that large carnivores are among the most iconic species, I anticipate that insights gleaned from ongoing and similar future studies will greatly inform public understanding and interest in apex predator behavior and conservation. It is my hope that this further inspires a groundswell change in improving the perception, and ultimately protection, of these ecologically critical species.

Bibliography

Adams, L.G. (2015) *Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: Progress Report (October 2013 - September 2014)*. Anchorage, AK.

Adams, L.G., Farley, S.D., Stricker, C. a, Demma, D.J., Roffler, G.H., Miller, D.C. & Rye, R.O. (2010) Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? *Ecological Applications*, **20**, 251–62.

Adams, L.G. & Roffler, G.H. (2010) *Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: Progress Report (October 2008 - September 2009)-Excerpt Regarding Seasonal Distribution of Caribou from This Progress Report*.

Alexander, R.M. (1984) The gaits of bipedal and quadrupedal animals. *The International Journal of Robotics Research*, **3**, 49–59.

Alexander, R.M. (1988) *Elastic Mechanisms in Animal Movement*. Cambridge University Press, Cambridge, England.

Alexander, R.M. (1990) Three uses for springs in legged locomotion. *The International Journal of Robotics Research*, **9**, 53–61.

Alexander, R.M. (2001) Damper for bad vibrations. *Nature*, **414**, 855–857.

Alexander, R.M. (2002) Tendon elasticity and muscle function. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, **133**, 1001–1011.

Alexander, R.M. (2005) Models and the scaling of energy costs for locomotion. *The Journal of Experimental Biology*, **208**, 1645–52.

Alexander, R.M. & Jayes, A.S. (1983) A dynamic similarity hypothesis for the gaits

of quadrupedal mamals. *Journal of Zoology*, **201**, 135–152.

Alexander, R.M. & Ker, R.F. (1990) Running is priced by the step. *Nature*, **346**, 220–221.

Alexander, S.M., Logan, T.B. & Paquet, P.C. (2006) Spatio-temporal co-occurrence of cougars (Felis concolor), wolves (Canis lupus) and their prey during winter: a comparison of two analytical methods. *Journal of Biogeography*, **33**, 2001–2012.

American Kennel Club. (2006) *The Complete Dog Book*, 20th ed. Ballantine Books.

Atwood, T.C., Gese, E.M. & Kunkel, K.E. (2007) Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. *The Journal of Wildlife Management*, **71**, 1098–1106.

Baigas, P.E., Olson, R.A., Nielson, R.M., Miller, S.N. & Lindzey, F.G. (2010) Modeling seasonal distribution and spatial capacity of moose in southeastern Wyoming. *Alces*, **46**, 89–112.

Ballard, W.B., Whitman, J.S. & Gardner, C.L. (1987) Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monographs*, **July**, 3–54.

Balme, G.A., Miller, J.R.B., Pitman, R.T. & Hunter, L.T.B. Caching reduces kleptoparasitism in a solitary, large felid. *Journal of Animal Ecology*.

Bangs, E. (2016) Lessons from wolf restoration in the northwestern U.S. *Intermountain Journal of Science*, **22**, 92–93.

Bartnick, T.D., Deelen, T.R. Van, Quigley, H.B. & Craighead, D. (2013) Variation in cougar (Puma concolor) predation habits during wolf (Canis lupus) recovery in

the southern Greater Yellowstone Ecosystem. *Canadian Journal of Zoology*, **93**, 82–93.

Beier, P. (2009) A Focal Species for Conservation Planning. *Puma: Ecology and Conservation* (eds M.G. Hornocker & S. Negri), pp. 177–189. University of Chicago Press.

Bennett, A.F. & Ruben, J.A. (1979) Endothermy and activity in vertebrates. *Science*, **206**, 649–54.

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P. & Saltz, D. (2011) Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology*, **22**, 236–239.

Berger, K.M. & Gese, E.M. (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, **76**, 1075–1085.

Bermingham, E.N., Thomas, D.G., Cave, N.J., Morris, P.J., Butterwick, R.F. & German, A.J. (2014) Energy requirements of adult dogs: A meta-analysis. *PLoS ONE*, **9**, e109681.

Beschta, R.L. & Ripple, W.J. (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, **142**, 2401–2414.

Beschta, R.L. & Ripple, W.J. (2012) The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology*, **157–158**, 88–98.

Bidder, O.R., Qasem, L. a & Wilson, R.P. (2012a) On higher ground: how well can dynamic body acceleration determine speed in variable terrain? *PloS one*, **7**, 1–7.

Bidder, O.R., Soresina, M., Shepard, E.L.C., Halsey, L.G., Quintana, F., Gómez-Laich, A. & Wilson, R.P. (2012b) The need for speed: testing acceleration for estimating animal travel rates in terrestrial dead-reckoning systems. *Zoology*, **115**, 58–64.

Bienwener, A.A. (1990) Biomechanics of mammalian terrestrial locomotion. *Science*, **250**, 1097–1103.

Biewener, A.A. (1989) Scaling body support in mammals: Limb posture and muscle mechanics. *Science*, **245**, 45–48.

Biewener, A.A. (1998) Muscle-tendon stresses and elastic energy storage during locomotion in the horse. *Comparative Biochemistry and Physiology - B Biochemistry and Molecular Biology*, **120**, 73–87.

Biewener, A.A. (2006) Patterns of mechanical energy change in tetrapod gait: Pendula, springs and work. *Journal of Experimental Zoology*, **911**, 899–911.

Blickhan. (1989) The spring-mass model for running and hopping. *Journal of Biomechanics*, **22**, 1217–1227.

Boisclair, D. & Leggett, W.C. (1989) The importance of activity in bioenergetics models applied to actively foraging fishes. *Canadian journal of fisheries and aquatic science*, **46**, 1859–1867.

Borg, B.L., Arthur, S.M., Bromen, N.A., Cassidy, K.A., McIntyre, R., Smith, D.W. & Prugh, L.R. (2016) Implications of harvest on the boundaries of protected areas

for large carnivore viewing opportunities. *Plos One*, **11**, e0153808.

Borg, B.L., Brainerd, S.M., Meier, T.J. & Prugh, L.R. (2015) Impacts of breeder loss on social structure, reproduction and population growth in a social canid. *The Journal of Animal Ecology*, **84**, 177–187.

Breed, G.A., Matthews, C.J.D., Marcoux, M., Higdon, J.W., LeBlanc, B., Petersen, S.D., Orr, J., Reinhart, N.R. & Ferguson, S.H. (2017) Sustained disruption of narwhal habitat use and behavior in the presence of Arctic killer whales. *Proceedings of the National Academy of Sciences*, **114**, 2628–2633.

Breiman, L. (2001) Random forests. *Machine Learning*, **45**, 5–32.

Brodie, E.D.I. & Brodie, E.D.J. (1999) Predator-prey arms races: Asymmetrical selection on predators and prey may be reduced when prey are dangerous. *BioScience*, **49**, 557–568.

Brown, D. (2009) Tracker Video Analysis and Modeling Tool.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Brown, D.D., Kays, R., Wikelski, M., Wilson, R. & Klimley, A. (2013) Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry*, **1**.

Bryce, C.M. & Williams, T.M. (2017) Comparative locomotor costs of domestic dogs reveal energetic economy of wolf-like breeds. *Journal of Experimental Biology*, **220**, 312–321.

Burch, J.W., Adams, L.G., Follmann, E.H. & Rexstad, E.A. (2005) Evaluation of

wolf density estimation from radiotelemetry data. *Wildlife Society Bulletin*, **33**, 1225–1236.

Burdett, C.L., Crooks, K.R., Theobald, D.M., Wilson, K.R., Boydston, E.E., Lyren, L.M., Fisher, R.N., Vickers, T.W., Morrison, S. a. & Boyce, W.M. (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. *Ecosphere*, **1**, 1–21.

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. (1999) Energetic constraints on the diet of terrestrial carnivores. *Nature*, **402**, 286–288.

Carbone, C., Pettorelli, N. & Stephens, P.A. (2011) The bigger they come, the harder they fall: body size and prey abundance influence predator-prey ratios. *Biology letters*, **7**, 312–5.

Carbone, C., Teacher, A. & Rowcliffe, J.M. (2007) The costs of carnivory. *PLoS Biology*, **5**, 363–368.

Careau, V., Réale, D., Humphries, M.M. & Thomas, D.W. (2010) The pace of life under artificial selection: Personality, energy expenditure, and longevity are correlated in domestic dogs. *The American Naturalist*, **175**, 753–8.

Carroll, C., Noss, R.F., Paquet, P.C. & Schumaker, N.H. (2003) Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecological Applications*, **13**, 1773–1789.

Cavagna, G.A., Franzetti, P., Heglund, N.C. & Willems, P. (1988) The determinants of the step frequency in running, trotting and hopping in man and other vertebrates. *Journal of Physiology*, 81–92.

Cavagna, G.A., Heglund, N.C. & Taylor, C.R. (1977) Mechanical work in terrestrial

locomotion: two basic mechanisms for minimizing energy expenditure.

American Journal of Physiology, **233**, R2430–R261.

Cavagna, G.A. & Kaneko, M. (1977) Mechanical work and efficiency in level

walking and running. *Journal of Physiology*, **268**, 467–481.

Central Alaska Network. (2015) *Weather & Climate Summary: Denali National Park

& Preserve Winter 2014-Fall 2015*.

Christianson, D. & Creel, S. (2014) Ecosystem scale declines in elk recruitment and

population growth with wolf colonization: A before-after-control-impact

approach. *PLoS ONE*, **9**, e102330.

Van Citters, R.L. & Franklin, D.L. (1969) Cardiovascular performance of Alaska sled

dogs during exercise. *Circulation Research*, **24**, 33–42.

Clutton-Brock, J. (1999) *A Natural History of Domesticated Mammals*, 2nd ed.

Cambridge University Press, Cambridge.

Combes, S.A., Iwasaki, J.M., Crall, J.D. & Rundle, D.E. (2012) Linking

biomechanics and ecology through predator-prey interactions: flight

performance of dragonflies and their prey. *Journal of Experimental Biology*,

215, 903–913.

Cooke, S.J., Hinch, S.G., Lucas, M.C. & Lutcavage, M. (2013) Biotelemetry and

Biologging. *Fisheries Techniques*, 3rd ed (eds A. V. Zale, D.L. Parrish & T.M.

Sutton), pp. 1–64. American Fisheries Society.

Cortez, M.H. (2011) Comparing the qualitatively different effects rapidly evolving

and rapidly induced defences have on predator-prey interactions. *Ecology Letters*, **14**, 202–209.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K., Creel, M., Winnie, J. & Maxwell, B. (2015) Elk alter habitat selection as an antipredator responsen to wolves. *Ecology*, **86**, 3387–3397.

Crête, M. & Larivière, S. (2003) Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology*, 1808–1814.

Dale, B.W., Adams, L.G. & Bowyer, R.T. (1994) Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology*, **63**, 644–652.

Dawkins, R. & Krebs, J.R. (1979) Arms races between and within species. *Proceedings of the Royal Society B: Biological Sciences*, **205**, 489–511.

Dickie, M., Serrouya, R., Mcnay, R.S. & Boutin, S. (2016) Faster and farther: Wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*.

Dickson, B.G., Jenness, J.S. & Beier, P. (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management*, **69**, 264–276.

Domenici, P. (2001) The scaling of locomotor performance in predator-prey encounters: From fish to killer whales. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, **131**, 169–182.

Domenici, P. & Blake, R.W. (1997) The kinematics and performance of fish fast-start

swimming. *The Journal of Experimental Biology*, **200**, 1165–1178.

Donadio, E. & Buskirk, S.W. (2006) Diet, morphology, and interspecific killing in carnivora. *The American Naturalist*, **167**, 524–36.

Downs, J.A., Heller, J.H., Loraamm, R., Oppenheim Stein, D., McDaniel, C. & Onorato, D.P. (2012) Accuracy of home range estimators for homogeneous and inhomogeneous point patterns. *Ecological Modelling*, **225**, 66–73.

Drake, A.G., Coquerelle, M. & Colombeau, G. (2015) 3D morphometric analysis of fossil canid skulls contradicts the suggested domestication of dogs during the late Paleolithic. *Nature Scientific Reports*, **5**, 1–8.

Duke, D. (2001) *Wildlife Use of Corridors in the Central Canadian Rockies: Multivariate Use of Habitat Characteristics and Trends in Corridor Use*. University of Alberta, Edmonton, Alberta.

Eggermann, J., Gula, R., Pirga, B., Theuerkauf, J., Tsunoda, H., Brzezowska, B., Rouys, S. & Radler, S. (2009) Daily and seasonal variation in wolf activity in the Bieszczady Mountains, SE Poland. *Mammalian Biology*, **74**, 159–163.

Elbroch, L.M., Lendrum, P.E., Newby, J., Quigley, H. & Thompson, D.J. (2015) Recolonizing wolves influence the realized niche of resident cougars. *Zoological Studies*, **54**, 41.

Elliott, J.P., Cowan, I.M. & Holling, C.S. (1977) Prey capture by the African lion. *Canadian Journal of Zoology*, **55**, 1811–1828.

Estensen, J., Borba, B. & Gleason, C. (2015) *2015 Yukon River Fall Season Summary*. Anchorage, AK.

Estes, J. a., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S. a., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, a. R.E., Soule, M.E., Virtanen, R. & Wardle, D. a. (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.

Fancy, S.G. & White, R.G. (1987) Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology*, **65**, 122–128.

Fedak, M.A., Rome, L. & Seeherman, H.J. (1981) One-step N2-dilution technique for calibrating open-circuit VO2 measuring systems. *Journal of applied physiology*, **51**, 772–776.

Figueirido, B., Martín-Serra, A., Tseng, Z.J. & Janis, C.M. (2015) Habitat changes and changing predatory habits in North American fossil canids. *Nature Communications*, **6**, 7976.

Fischer, M.S. & Lilje, K.E. (2011) *Dogs in Motion*. VDH Service GmbH.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B. & Beyer, H.L. (2004) Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology*, **41**, 201–212.

Freedman, A.H., Gronau, I., Schweizer, R.M., Ortega-Del Vecchyo, D., Han, E., Silva, P.M., Galaverni, M., Fan, Z., Marx, P., Lorente-Galdos, B., Beale, H., Ramirez, O., Hormozdiari, F., Alkan, C., Vilà, C., Squire, K., Geffen, E., Kusak, J., Boyko, A.R., Parker, H.G., Lee, C., Tadigotla, V., Siepel, A., Bustamante,

C.D., Harkins, T.T., Nelson, S.F., Ostrander, E.A., Marques-Bonet, T., Wayne, R.K. & Novembre, J. (2014) Genome sequencing highlights the dynamic early history of dogs. *PLoS Genetics*, **10**, e1004016.

Fuller, T.K. (1989) Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs*, **Oct**, 3–41.

Fuller, T.K., Mech, L.D. & Cochrane, J.F. (2003) Wolf Population Dynamics. *Wolves: Behavior, Ecology & Conservation* (eds L.D. Mech & L. Boitani), pp. 161–191. University of Chicago Press.

Galibert, F., Quignon, P., Hitte, C. & André, C. (2011) Toward understanding dog evolutionary and domestication history. *Comptes Rendus - Biologies*, **334**, 190–196.

Gallagher, A.J., Creel, S., Wilson, R.P. & Cooke, S.J. (2017) Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution*, **32**, 88–96.

Garland, T.J. (1983) Scaling the ecological cost of transport to body mass in terrestrial mammals. *The American Naturalist*, **121**, 571–587.

Gerth, N., Redman, P., Speakman, J., Jackson, S. & Starck, J.M. (2010) Energy metabolism of Inuit sled dogs. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, **180**, 577–89.

Gese, E.M. (2001) Monitoring of Terrestrial Carnivore Populations. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D.W. MacDonald & R.K. Wayne), pp. 372–396. Cambridge University Press.

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C.

(2007) LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS one*, **2**, e207.

Gforces.net. (2010) Some Typical Examples of G Forces. URL http://www.gforces.net/ [accessed 1 January 2016]

Gillooly, J.F., Gomez, J.P. & Mavrodiev, E. V. (2017) A broad-scale comparison of aerobic activity levels in vertebrates: endotherms versus ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20162328.

Girard, I. (2001) Field cost of activity in the kit fox, Vulpes macrotis. *Physiological and Biochemical Zoology*, **74**, 191–202.

Gittleman, J.L. (1989) Carnivore Group Living: Comparative Trends. *Carnivore Behavior, Ecology and Evolution* (ed J.L. Gittleman), pp. 183–207. Cornell University Press, New York, NY.

Gleiss, A.C., Wilson, R.P. & Shepard, E.L.C. (2011) Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, **2**, 23–33.

Glowacinski, Z. & Profus, P. (1997) Potential impact of wolves Canis lupus on prey populatiosn in eastern Poland. *Biological Conservation*, **3207**, 99–106.

Gomeñuka, N. a, Bona, R.L., da Rosa, R.G. & Peyré-Tartaruga, L. a. (2014) Adaptations to changing speed, load, and gradient in human walking: cost of transport, optimal speed, and pendulum. *Scandinavian Journal of Medicine & Science in Sports*, **24**, e165-73.

Gomeñuka, N.A., Bona, R.L., da Rosa, R.G. & Peyré-Tartaruga, L.A. (2016) The

pendular mechanism does not determine the optimal speed of loaded walking on gradients. *Human Movement Science*, **47**, 175–185.

Gómez Laich, A., Wilson, R.P., Gleiss, A.C., Shepard, E.L.C. & Quintana, F. (2011) Use of overall dynamic body acceleration for estimating energy expenditure in cormorants. Does locomotion in different media affect relationships? *Journal of Experimental Marine Biology and Ecology*, **399**, 151–155.

Gorman, M.L., Mills, M.G., Raath, J.P. & Speakman, J.R. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, **852**, 479–481.

Gray, J. (1968) *Animal Locomotion*. W.W. Norton & Company, Inc, New York.

Green, J. a, Halsey, L.G., Wilson, R.P. & Frappell, P.B. (2009) Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *The Journal of Experimental Biology*, **212**, 471–82.

Gregersen, C.S., Silverton, N. a & Carrier, D.R. (1998) External work and potential for elastic storage at the limb joints of running dogs. *The Journal of Experimental Biology*, **201**, 3197–210.

Griffin, T.M., Main, R.P. & Farley, C.T. (2004) Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements? *The Journal of Experimental Biology*, **207**, 3545–58.

Haber, G. (1977) *Socio-Ecological Dynamics of Wolves and Prey In a Subarctic Ecosystem*. University of British Columbia, Vancouver.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421–425.

Halsey, L.G. (2011) The challenge of measuring energy expenditure: Current field and laboratory methods. *Comparative Biochemistry and Physiology, Part A*, **158**, 247–251.

Halsey, L.G. (2013) The relationship between energy expenditure and speed during pedestrian locomotion in birds: A morphological basis for the elevated y-intercept? *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, **165**, 295–298.

Halsey, L.G. (2016) Terrestrial movement energetics: current knowledge and its application to the optimising animal. *The Journal of Experimental Biology*, **219**, 1424–1431.

Halsey, L.G., Shepard, E.L.C., Quintana, F., Gomez Laich, A., Green, J. a & Wilson, R.P. (2009) The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, **152**, 197–202.

Halsey, L.G., Shepard, E.L.C. & Wilson, R.P. (2011) Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, **158**, 305–14.

Halsey, L.G. & White, C.R. (2017) A different angle: comparative analyses of whole-animal transport costs when running uphill. *Journal of Experimental Biology*,

220, 161–166.

Hammond, K.A., Konarzewski, M., Torres, R.M. & Diamond, J. (1994) Metabolic ceilings under a combination of peak energy demands. *Physiological Zoology*, **67**, 1479–1506.

Hayes, R.D., Baer, A.M., Wotschikowsky, U. & Harestad, A.S. (2000) Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology*, **78**, 49–59.

Hayes, R.D. & Harestad, A.S. (2000) Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology*, **78**, 60–66.

Hayssen, V. & van Tienhoven, A. (1993) *Asdell's Patterns of Mammalian Reproduction*. Combstock Publishing Associats, Ithaca, NY.

Hebblewhite, M. & Merrill, E. (2008) Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, **45**, 834–844.

Hebblewhite, M., Merrill, E.H. & McDonald, T.L. (2005) Spatial decomposition of predation risk using resource selection functions: An example in a wolf-elk predator-prey system. *Oikos*, **111**, 101–111.

Hedenström, A. & Rosén, M. (2001) Predator versus prey: on aerial hunting and escape strategies in birds. *Behavioral Ecology*, **12**, 150–156.

Heglund, N.C. & Taylor, C.R. (1988) Speed, stride frequency and energy cost per stride: How do they change with body size and gait? *Journal of Experimental Biology*, **138**, 301–318.

Hermanson, J.W. (1997) Architecture and the division of labor in the extensor capri

radialis muscle of horses. *Acta Anatomica*, **159**, 127–135.

Hinchcliff, K.W., Reinhart, G.A., Burr, J.R., Schreier, C.J. & Swenson, R.A. (1997) Metabolizable energy intake and sustained energy expenditure of Alaskan sled dogs during heavy exertion in the cold. *American Journal of Veterinary Research*, **58**, 1457–62.

Hornocker, M.G. (1970) An analysis of mountain lion predation on mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs*, **21**, 3–39.

Hornocker, M. & Negri, S. (eds). (2009) *Cougar: Ecology and Conservation*. University of Chicago Press, Chicago.

Howland, H.C. (1974) Optimal strategies for predator avoidance: The relative importance of speed and manoeuvrability. *Journal of Theoretical Biology*, **47**, 333–350.

Hoyt, D.F. & Taylor, C.R. (1981) Gait and the energetics of locomotion in horses. *Nature*, **292**, 239–240.

Hoyt, D.F., Wickler, S.J. & Cogger, E. a. (2000) Time of contact and step length: the effect of limb length, running speed, load carrying and incline. *The Journal of Experimenal Biology*, **203**, 221–227.

Hoyt, D.F., Wickler, S.J., Dutto, D.J., Catterfeld, G.E. & Johnsen, D. (2006) What are the relations between mechanics, gait parameters, and energetics in terrestrial locomotion? *Journal of Experimental Zoology*, **922**, 912–922.

Huggard, D.J. (1993) Effect of snow depth on predation and scavenging by gray wolves. *Journal of Wildlife Management*, **57**, 382–388.

Humphries, M.M. & McCann, K.S. (2014) Metabolic ecology. *The Journal of Animal Ecology*, **83**, 7–19.

Huson, H.J., Parker, H.G., Runstadler, J. & Ostrander, E.A. (2010) A genetic dissection of breed composition and performance enhancement in the Alaskan sled dog. *BMC Genetics*, **11**, 71.

Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R. & Quigley, H. (2003) Assessing differential prey selection patterns between two sympatric large carnivores. *OIKOS*, **101**, 591–601.

IUCN. (2016) IUCN Red List Status. URL http://www.iucnredlist.org/initiatives/mammals/analysis/red-list-status [accessed 3 February 2017]

Jalkotzy, M.G., Ross, P.I. & Wierzchowski, J. (2002) Regional scale cougar habitat modeling in Southwestern Alberta, Canada. *Proceedings of the Sixth Mountain Lion Workshop*, p. Texas Parks and Wildlife Department, Austin.

James, A.R.C. & Stuart-Smith, A.K. (2000) Distribution of caribou and wolves in relation to linear corridors. *The Journal of Wildlife Management*, **64**, 154–159.

Jayes, A.S. & Alexander, R.M. (1978) Mechanics of locomotion of dogs and sheep. *Journal of Zoology*, **185**, 289–308.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B. & Okarma, H. (2001) Daily movements and territory use by radio-collared wolves (Canis lupus) in Bialowieza Primeval Forest in Poland. *Canadian Journal of Zoology*, **79**, 1993–2004.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., Selva, N., Zub, K. & Szymura, L. (2002) Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). *Ecology*, **83**, 1341–1356.

Jimenez, A.G. (2016) Physiological underpinnings in life-history trade-offs in man's most popular selection experiment: the dog. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, **186**, 813–827.

Kaczensky, P., Hayes, R.D. & Promberger, C. (2005) Effect of raven Corvus corax scavenging on the kill rates of wolf Canis lupus packs. *Wildlife Biology*, **11**, 101–108.

Kar, D.C., Kurien Issac, K. & Jayarajan, K. (2003) Gaits and energetics in terrestrial legged locomotion. *Mechanism and Machine Theory*, **38**, 355–366.

Karanth, K.U. & Sunquist, M.E. (1995) Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology*, **64**, 439–450.

Karasov, W.H. (1992) Daily energy expenditure and the cost of activity in mammals. *American Zoologist*, **32**, 238–248.

Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, **10**, 690–700.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and planet. *Science*, **348**, aaa2478-1-aaa2478-9.

Keith, L.B. (1983) Population dynamics of wolves. *Wolves of Canada and Alaska: their status, biology and management*, Report Ser (ed L.N. Carbyn), pp. 66–77.

Canadian Wildlife Service, Edmonton, Alberta, Canada.

Kemp, T.J., Bachus, K.N., Nairn, J. a & Carrier, D.R. (2005) Functional trade-offs in the limb bones of dogs selected for running versus fighting. *The Journal of Experimental Biology*, **208**, 3475–82.

Ker, R.F. (1981) Dynamic tensile properties of the plantaris tendon of sheep (Ovis aries). *The Journal of Experimental Biology*, **93**, 283–302.

King, S.L., Schick, R.S., Donovan, C., Booth, C.G., Burgman, M., Thomas, L. & Harwood, J. (2015) An interim framework for assessing the population consequences of disturbance. *Methods in Ecology and Evolution*, **6**, 1150–1158.

Kleiber, M. (1961) *The Fire of Life: An Introduction to Animal Energetcis*. John Wiley & Sons, Inc., New York, NY.

Kleiman, D.G. & Eisenberg, J.F. (1973) Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour*, **21**, 637–659.

Kleiman, D.G., Geist, V. & McDade, M.C. (eds). (2003) *Grzimek's Animal Life Encyclopedia: Mammals*, 2nd ed. Gale.

Koehler, G.M. & Hornocker, M.G. (1991) Seasonal resource use among mountain lions, bobcats, and coyotes. *Journal of Mammalogy*, **72**, 391–396.

Kortello, A.D., Hurd, T.E. & Murray, D.L. (2007) Interactions between cougars (Puma concolor) and gray wolves (Canis lupus) in Banff National Park, Alberta. *Ecoscience*, **14**, 214–222.

Koteja, P. (1987) On the relation between basal and maximum metabolic rate in mammals. *Comparative Biochemistry and Physiology. A, Comparative*

physiology, **87**, 205–8.

Kram, R. & Taylor, R. (1990) Energetics of running: A new perspective. *Nature*, **346**, 265–267.

Kramer, D.L. & McLaughlin, R.L. (2001) The behavioral ecology of intermittent locomotion. *American Zoologist*, **153**, 137–153.

Kreeger, T.J. (2003) The internal wolf: Physiology, pathology & pharmacology. *Wolves: Behavior, Ecology & Conservation*, First (eds L.D. Mech & L. Boitani), pp. 192–217. University of Chicago Press, Chicago.

Krumm, C.E., Conner, M.M., Hobbs, N.T., Hunter, D.O. & Miller, M.W. (2010) Mountain lions prey selectively on prion-infected mule deer. *Biology Letters*, **6**, 209–211.

Kunkel, K.E., Ruth, T.K., Pletscher, D.H. & Hornocker, M.G. (1999) Winter prey selection by wolves and cougars in and near Glacier National Park Monatana. *The Journal of Wildlife Management*, **63**, 901–910.

Laing, S.P. & Lindzey, F.P. (1991) Cougar habitat selection in south-central Utah. *Mounting Lion-human Interaction Symposium and Workshop* (ed C.E. Braun), pp. 86–94. Colorado Division of Wildlife, Denver.

Lande, R. (1988) Genetics and demography in biological conservation. *Science*, **241**, 1455–1460.

Larson, G., Karlsson, E.K., Perri, A., Webster, M.T., Ho, S.Y.W., Peters, J., Stahl, P.W., Piper, P.J., Lingaas, F., Fredholm, M., Comstock, K.E., Modiano, J.F., Schelling, C., Agoulnik, A.I., Leegwater, P. a, Dobney, K., Vigne, J.-D., Vilà,

C., Andersson, L. & Lindblad-Toh, K. (2012) Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 8878–83.

LaRue, M.A., Nielsen, C.K., Dowling, M., Miller, K., Wilson, B., Shaw, H. & Anderson, C.R. (2012) Cougars are recolonizing the midwest: Analysis of cougar confirmations during 1990-2008. *Journal of Wildlife Management*, **76**, 1364–1369.

Latham, A.D.M., Latham, M.C., Boyce, M.S. & Boutin, S. (2011) Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications*, **21**, 2854–2865.

Laundré, J.W. (2014) How large predators manage the cost of hunting. *Science*, **346**, 33–34.

Laundré, J.W. & Hernández, L. (2003) Winter hunting habitat of pumas (Puma concolor) in northwestern Utah and southern Idaho, USA. *Wildlife Biology*, **9**, 123–129.

Lechner, A.J. (1978) The scaling of maximal oxygen consumption and pulmonary dimensions in small mammals. *Respiration Physiology*, **34**, 29–44.

Levi, T. & Wilmers, C.C. (2012) Wolves – coyotes – foxes: a cascade among carnivores. *Ecology*, **93**, 921–929.

Lewis, L.D. (1995) *Equine Clinical Nutrition: Feeding and Care*. Wiley-Blackwell.

Liberga, O., Aronson, Å., Sanda, H., Wabakkenc, P., Maartmannc, E., Svensson, L. & Åkesson, M. (2012) Monitoring of wolves in Scandinavia. *Hystrix*, **23**, 35–48.

Lindblad-Toh, K., Wade, C.M., Mikkelsen, T.S., Karlsson, E.K., Jaffe, D.B., Kamal, M., Clamp, M., Chang, J.L., Kulbokas, E.J., Zody, M.C., Mauceli, E., Xie, X., Breen, M., Wayne, R.K., Ostrander, E. a, Ponting, C.P., Galibert, F., Smith, D.R., DeJong, P.J., Kirkness, E., Alvarez, P., Biagi, T., Brockman, W., Butler, J., Chin, C.-W., Cook, A., Cuff, J., Daly, M.J., DeCaprio, D., Gnerre, S., Grabherr, M., Kellis, M., Kleber, M., Bardeleben, C., Goodstadt, L., Heger, A., Hitte, C., Kim, L., Koepfli, K.-P., Parker, H.G., Pollinger, J.P., Searle, S.M.J., Sutter, N.B., Thomas, R., Webber, C., Baldwin, J., Abebe, A., Abouelleil, A., Aftuck, L., Ait-Zahra, M., Aldredge, T., Allen, N., An, P., Anderson, S., Antoine, C., Arachchi, H., Aslam, A., Ayotte, L., Bachantsang, P., Barry, A., Bayul, T., Benamara, M., Berlin, A., Bessette, D., Blitshteyn, B., Bloom, T., Blye, J., Boguslavskiy, L., Bonnet, C., Boukhgalter, B., Brown, A., Cahill, P., Calixte, N., Camarata, J., Cheshatsang, Y., Chu, J., Citroen, M., Collymore, A., Cooke, P., Dawoe, T., Daza, R., Decktor, K., DeGray, S., Dhargay, N., Dooley, K., Dooley, K., Dorje, P., Dorjee, K., Dorris, L., Duffey, N., Dupes, A., Egbiremolen, O., Elong, R., Falk, J., Farina, A., Faro, S., Ferguson, D., Ferreira, P., Fisher, S., FitzGerald, M., Foley, K., Foley, C., Franke, A., Friedrich, D., Gage, D., Garber, M., Gearin, G., Giannoukos, G., Goode, T., Goyette, A., Graham, J., Grandbois, E., Gyaltsen, K., Hafez, N., Hagopian, D., Hagos, B., Hall, J., Healy, C., Hegarty, R., Honan, T., Horn, A., Houde, N., Hughes, L., Hunnicutt, L., Husby, M., Jester, B., Jones, C., Kamat, A., Kanga, B., Kells, C., Khazanovich, D., Kieu, A.C., Kisner, P., Kumar, M., Lance, K., Landers, T.,

Lara, M., Lee, W., Leger, J.-P., Lennon, N., Leuper, L., LeVine, S., Liu, J., Liu, X., Lokyitsang, Y., Lokyitsang, T., Lui, A., Macdonald, J., Major, J., Marabella, R., Maru, K., Matthews, C., McDonough, S., Mehta, T., Meldrim, J., Melnikov, A., Meneus, L., Mihalev, A., Mihova, T., Miller, K., Mittelman, R., Mlenga, V., Mulrain, L., Munson, G., Navidi, A., Naylor, J., Nguyen, T., Nguyen, N., Nguyen, C., Nguyen, T., Nicol, R., Norbu, N., Norbu, C., Novod, N., Nyima, T., Olandt, P., O'Neill, B., O'Neill, K., Osman, S., Oyono, L., Patti, C., Perrin, D., Phunkhang, P., Pierre, F., Priest, M., Rachupka, A., Raghuraman, S., Rameau, R., Ray, V., Raymond, C., Rege, F., Rise, C., Rogers, J., Rogov, P., Sahalie, J., Settipalli, S., Sharpe, T., Shea, T., Sheehan, M., Sherpa, N., Shi, J., Shih, D., Sloan, J., Smith, C., Sparrow, T., Stalker, J., Stange-Thomann, N., Stavropoulos, S., Stone, C., Stone, S., Sykes, S., Tchuinga, P., Tenzing, P., Tesfaye, S., Thoulutsang, D., Thoulutsang, Y., Topham, K., Topping, I., Tsamla, T., Vassiliev, H., Venkataraman, V., Vo, A., Wangchuk, T., Wangdi, T., Weiand, M., Wilkinson, J., Wilson, A., Yadav, S., Yang, S., Yang, X., Young, G., Yu, Q., Zainoun, J., Zembek, L., Zimmer, A. & Lander, E.S. (2005) Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature*, **438**, 803–19.

Linnell, J.D.C. & Strand, O. (2000) Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, **6**, 169–176.

Logan, K.A. & Irwin, L.L. (1985) Mountain lion habitats in the Big Horn Mountains, Wyoming. *Wildlife Society Bulletin*, **13**, 257–262.

Macdonald, D.W. & Sillero-Zubiri, C. (2004) Dramatis personae: Wild canids-an introduction and dramatis personae. *Biology and conservation of wild canids* (eds D.W. Macdonald & C. Sillero-Zubiri), pp. 3–36. Oxford University Press, Oxford.

MacNulty, D.R., Mech, L.D. & Smith, D.W. (2007) A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy*, **88**, 595–605.

MacNulty, D.R., Smith, D.W., Mech, L.D. & Eberly, L.E. (2009) Body size and predatory performance in wolves: is bigger better? *The Journal of Animal Ecology*, **78**, 532–9.

MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J. a. & Packer, C. (2011) Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology*, **23**, 75–82.

MacNulty, D.R., Tallian, A., Stahler, D.R. & Smith, D.W. (2014) Influence of group size on the success of wolves hunting bison. *PloS one*, **9**, e112884.

Maes, L.D., Herbin, M., Hackert, R., Bels, V.L. & Abourachid, A. (2008) Steady locomotion in dogs: temporal and associated spatial coordination patterns and the effect of speed. *The Journal of Experimental Biology*, **211**, 138–49.

Maresh, J.L., Fish, F.E., Nowacek, D.P., Nowacek, S.M. & Wells, R.S. (2004) High performance turning capabilities during foraging by bottlenose dolphins (Tursiops Truncatus). *Marine Mammal Science*, **20**, 498–509.

McNab, B.K. (2002) The Significance of Energetics for the Population Ecology of

Vertebrates. *The Physiological Ecology of Vertebrates: A View from Energetics*, pp. 431–446. Cornell University Press, Ithaca, NY.

McPhee, H.M., Webb, N.F. & Merrill, E.H. (2012) Hierarchial predation: wolf (Canis lupus) selection along hunt paths and at kill sites. *Canadian Journal of Zoology*, **90**, 555–563.

Mech, L.D. (1970) *The Wolf: The Behavior and Ecology of an Endangered Species*. Natural History Press, New York.

Mech, L.D. (1988) *The Arctic Wolf: Living with the Pack*. Voyageur Press, Stillwater, MN.

Mech, L.D. (1994) Regular and homeward travel speeds of Arctic wolves. *Journal of Mammalogy*, **75**, 741–742.

Mech, L.D. (2012) Gray wolf (Canis lupus) movements and behavior around a kill site and implications for GPS collar studies. *Canadian Field-Naturalist*, **125**, 353–356.

Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W. & Dale, B.W. (1998) *The Wolves of Denali*. University of Minnesota Press.

Mech, L.D. & Boitani, L. (eds). (2003a) *Wolves: Behavior, Ecology & Conservation*. University of Chicago Press.

Mech, L.D. & Boitani, L. (2003b) Wolf Social Ecology. *Wolves: Behavior, Ecology & Conservation* (eds L.D. Mech & L. Boitani), pp. 1–34. University of Chicago Press.

Mech, L.D. & Cluff, H.D. (2009) Long daily movements of wolves, Canis lupus,

during pup rearing. *Canadian Field-Naturalist*, **123**, 68–69.

Mech, L.D. & Cluff, H.D. (2011) Movements of wolves at the northern extreme of the species' range, including during four months of darkness. *PLoS ONE*, **6**, 2–6.

Mech, L.D. & Korb, M. (1978) An unusually long pursuit of a deer by a wolf. *Journal of Mammalogy*, **59**, 860–861.

Mech, L.D., Meier, T.J., Burch, J.W. & Adams, L.G. (1995) Patterns of prey selection by wolves in Denali National Park, Alaska. *Ecology & Conservation of Wolves in a Changing World* (eds L.N. Carbyn, S.H. Fritts & D.R. Seip), pp. 231–244. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.

Mech, L.D. & Peterson, R.O. (2003) Wolf-Prey Relations. *Wolves: Behavior, Ecology & Conservation* (eds L.D. Mech & L. Boitani), pp. 131–160. University of Chicago Press, Chicago.

Mech, L.D., Smith, D.W. & Macnulty, D.R. (eds). (2015a) *Wolves on the Hunt*. University of Chicago Press, Chicago.

Mech, L.D., Smith, D.W. & MacNulty, D.R. (2015b) Introduction: The Wolf As a Killing Machine. *Wolves On the Hunt: The Behavior of Wolves Hunting Wild Prey*, p. University of Chicago Press.

Meier, T.J. & Burch, J.W. (2009) *Wolf Monitoring Protocol for Denali National Park and Preserve, Yukon-Charley Rivers National Preserve and Wrangell-St. Elias National Park and Preserve*. Fort Collins, CO.

Miller, B.F., Drake, J.C., Peelor, F.F., Biela, L.M., Geor, R.J., Hinchcliff, K.W., Davis, M. & Hamilton, K.L. (2014) Participation in a 1000-mile race increases

the oxidation of carbohydrate in Alaskan sled dogs. *Journal of Applied Physiology*, **118**, 1502–1509.

Miller, B.F., Ehrlicher, S.E., Drake, J.C., Peelor, F.F., Biela, L.M., Pratt-Phillips, S., Davis, M., Hamilton, K.L., Frederick, F., Biela, L.M., Pratt-Phillips, S., Davis, M., Karyn, L., Science, E., Collins, F., Investigators, C., Miller, B.F. & Science, E. (2015) Assessment of protein synthesis in highly aerobic canine species at the onset and during exercise training. *Journal of Applied Physiology*, **118**, 811–817.

Di Minin, E., Slotow, R., Hunter, L.T.B., Montesino Pouzols, F., Toivonen, T., Verburg, P.H., Leader-Williams, N., Petracca, L. & Moilanen, A. (2016) Global priorities for national carnivore conservation under land use change. *Scientific Reports*, **6**, 1–9.

Miquelle, D.G., Stephens, P.A., Smirnov, E.N., Goodrich, J.M., Zaumyslova, O.J. & Myslenkov, A.E. (2005) Tigers and wolves in the Russian Far East: Competitive exclusion, functional redundancy, and conservation implications. *Large Carnivores and the Conservation of Biodiversity* (eds J.C. Ray, K.H. Redford, R.S. Steneck & J. Berger), pp. 179–207. Island Press.

Morrison, J.C., Sechrest, W., Dinerstein, E., Wilcove, D.S. & Lamoreux, J.F. (2007) Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy*, **88**, 1363–1380.

Murie, A. (1944) *The Wolves of Mount McKinley*, Fauna of t. US National Park Service, Washington, DC.

Murphy, K. & Ruth, T.K. (2009) Diet and prey selection of a perfect predator.

Cougar: Ecology & Conservation, 1st ed (eds M. Hornocker & S. Negri), pp. 118–137. University of Chicago Press.

Murray, D.L. & Lariviere, S. (2002) The relationship between foot size of wild canids and regional snow conditions: Evidence for selection against a high footload? *Journal of Zoology*, **256**, 289–299.

Nagy, K. (1994) Field bioenergetics of mammals - What determines field metabolic rates. *Australian Journal of Zoology*, **42**, 43–53.

Nagy, K.A., Girard, I.A. & Brown, T.K. (1999) Energetics of free ranging mammals, reptiles, and birds. *Annual Review of Nutrition*, 247–277.

Nanua, P. & Waldron, K. (1995) Energy comparison between trot, bound, and gallop using a simple model. *Journal of Biomechanical Engineering*, **117**, 466–473.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, **105**, 19052–19059.

Nathan, R., Spiegel, O., Fortmann-roe, S., Harel, R., Wikelski, M. & Getz, W.M. (2012) Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology*, **215**, 986–996.

National Research Council. (2006) *Nutrient Requirements of Dogs and Cats*. National Academies Press, Washington, DC.

New, L., Clark, J., Costa, D., Fleishman, E., Hindell, M., Klanjšček, T., Lusseau, D., Kraus, S., McMahon, C., Robinson, P., Schick, R., Schwarz, L., Simmons, S.,

Thomas, L., Tyack, P. & Harwood, J. (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Marine Ecology Progress Series*, **496**, 99–108.

Newsome, T.M. & Ripple, W.J. (2014) A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology*, **84**, 49–59.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T. & Paquet, P.C. (1996) Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, **10**, 949–963.

Okarma, H., Jedrzejewski, W., Schmidt, K., Kowalczyk, R. & Jedrzejewska, B. (1997) Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. *Acta Theriologica*, **42**, 203–224.

Okarma, H. & Koteja, P. (1987) Basal metabolic rate of the gray wolf in Poland. *Journal of Wildlife Management*, **51**, 800–801.

Ordiz, A., Bischof, R. & Swenson, J.E. (2013) Saving large carnivores, but losing the apex predator? *Biological Conservation*, **168**, 128–133.

Oriol-cotterill, A., Valeix, M., Frank, L.G., Riginos, C. & Macdonald, D.W. (2015) Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, **124**, 1263–1273.

Packard, J.M. (2003) Wolf behavior: reproductive, social, and intelligent. *Wolves: Behavior, Ecology & Conservation* (eds L.D. Mech & L. Boitani), pp. 35–65. University of Chicago Press, Chicago.

Packard, G.C. & Boardman, T.J. (1999) The use of percentages and size-specific indices to normalize physiological data for variation in body size: Wasted time, wasted effort? *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, **122**, 37–44.

Pagan, J. & Hintz, H. (1986) Energy expenditure in horses during submaximal exercise. *Journal of Animal Science*, **63**, 822–830.

Pagano, A.M., Rode, K.D., Cutting, A., Owen, M.A., Jensen, S., Ware, J. V, Robbins, C.T., Durner, G.M., Atwood, T.C., Obbard, M.E., Middel, K.R., Thiemann, G.W. & Williams, T.M. (2017) Using tri-axial accelerometers to identify wild polar bear behaviors. *Endangered Species Research*, **32**, 19–33.

Paine, R.T. (1980) Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, **49**, 666–685.

Parker, H.G. (2012) Genomic analyses of modern dog breeds. *Mammalian Genome*, **23**, 19–27.

Parker, H.G., Kim, L. V., Sutter, N.B., Carlson, S., Lorentzen, T.D., Malek, T.B., Johnson, G.S., DeFrance, H.B., Ostrander, E.A. & Kruglyak, L. (2004) Genetic structure of the purebred domestic dog. *Science*, **304**, 1160–1164.

Pasi, B.M. & Carrier, D.R. (2003) Functional trade-offs in the limb muscles of dogs selected for running vs. fighting. *Journal of Evolutionary Biology*, **16**, 324–32.

Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbeg, B., Orrock, J.L., Peacor, S.D., Preisser, E.L., Schmitz, O.J. & Trussell, G.C. (2008) Revisiting the classics: Considering nonconsumptive effects in textbook

examples of predator – prey interactions. *Ecology*, **89**, 2416–2425.

Perri, A. (2016) A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation. *Journal of Archaeological Science*, **68**, 1–4.

Perry, A.K., Blickhan, R., Biewener, A.A., Heglund, N.C. & Taylor, C.R. (1988) Preferred speeds in terrestrial vertebrates: Are they equivalent? *Journal of Experimental Biology*, **137**, 207–219.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Peterson, R.O. & Allen, D.L. (1974) Snow conditions as a parameter in moose–wolf relationships. *Naturaliste Canadien*, 481–492.

Peterson, R.O. & Ciucci, P. (2003) The Wolf as a Carnivore. *Wolves: Behavior, Ecology & Conservation* (eds L.D. Mech & L. Boitani), pp. 104–130. University of Chicago Press.

Peterson, R.O., Jacobs, A.K., Drummer, T.D., Mech, L.D. & Smith, D.W. (2002) Leadership behavior in relation to dominance and reproductive status in gray wolves, Canis lupus. *Canadian Journal of Zoology*, **80**, 1405–1412.

Pionnier-Capitan, M., Bemilli, C., Bodu, P., Célérier, G., Ferrié, J.G., Fosse, P., Garcià, M. & Vigne, J.D. (2011) New evidence for Upper Palaeolithic small domestic dogs in South-Western Europe. *Journal of Archaeological Science*, **38**, 2123–2140.

Podgórski, T., Schmidt, K., Kowalczyk, R. & Gulczyñska, A. (2008) Microhabitat selection by Eurasian lynx and its implications for species conservation. *Acta*

Theriologica, **53**, 97–110.

Pontzer, H. (2016) A unified theory for the energy cost of legged locomotion. *Biology Letters*, **12**, 1–5.

Poole, D.C. & Erickson, H.H. (2011) Highly athletic terrestrial mammals: horses and dogs. *Comprehensive Physiology*, **1**, 1–37.

Post, E., Forchhammer, M.C., Bret-harte, M.S., Callaghan, T. V, Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., Mcguire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., Wal, R. Van Der, Welker, J., Wookey, P.A., Schmidt, N.M. & Aastrup, P. (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science*, **325**, 1355–1358.

Post, E., Peterson, R.O., Stenseth, N.C. & Mclaren, B.E. (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.

Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L.G., Shepard, E.L.C., Gleiss, A.C. & Wilson, R. (2012) Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PloS one*, **7**, e31187.

Raab, J.L., Eng, P. & Waschler, R.A. (1976) Metabolic cost of grade running in dogs. *Journal of applied physiology*, **41**, 532–5.

R Core Team. (2014) R: A language and environment for statistical computing.

Rattenbury, K.L. (2011) *FY11 NPS Dall's Sheep Surveys – ARCN and CAKN Park Units*. Fairbanks, AK.

Ray, J.C., Redford, K.H., Steneck, R.S. & Berger, J. (eds). (2005) *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington DC.

Reichman, O.J. & Aitchinson, S. (1981) Mammal trails on mountain slopes: Optimal paths in relation to slope angle and body weight. *The American Naturalist*, **117**, 416–420.

Reilly, S.M., McElroy, E.J. & Biknevicius, A.R. (2007) Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. *Zoology*, **110**, 271–289.

Renecker, J. & Schwartz, C. (1997) Food habits and feeding behavior. *Ecology and Management of the North American Moose* (eds A. Franzmann & C. Schwartz), p. Smithsonian Institute Press, London, United Kingdom.

Rennick, P. (ed). (1987) *Dogs of the North*. Alaska Geographic Society, Anchorage, AK.

Rezende, E.L., Gomes, F.R., Chappell, M.A. & Garland Jr., T. (2009) Running behavior and its energy cost in mice selectively bred for high voluntary locomotor activity. *Physiological and Biochemical Zoology*, **82**, 662–679.

Ripple, W.J. & Beschta, R.L. (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience*, **54**, 755–766.

Ripple, W.J., Beschta, R.L. & Painter, L.E. (2015) Trophic cascades from wolves to

alders in Yellowstone. *Journal of Animal Ecology*, **354**, 254–260.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 151–163.

Ripple, W.J., Wirsing, A.J., Wilmers, C.C. & Letnic, M. (2013) Widespread mesopredator effects after wolf extirpation. *Biological Conservation*, **160**, 70–79.

Rosenzweig, M.L. (1966) Community structure in sympatric carnivora. *Journal of Mammalogy*, **47**, 602–612.

Ruben, J.A. (2010) *The Role of the Vertebral Column during Jumping in Quadrupedal Mammals*. Oregon State University.

Ruth, T.S. (2004) *Patterns of Resource Use among Cougars and Wolves in Northwestern Montana and Southeastern British Columbia*. University of Idaho, Moscow, Idaho.

Ruth, T.K., Haroldson, M.A., Murphy, K.M., Buotte, P.C., Hornocker, M.G. & Quigley, H.B. (2011) Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. *Journal of Wildlife Management*, **75**, 1381–1398.

Ruth, T. & Murphy, K. (2009a) Cougar-prey relationships. *Cougar: Ecology & Conservation* (eds M. Hornocker & S. Negri), pp. 138–162. University of Chicago Press, Chicago.

Ruth, T. & Murphy, K. (2009b) Competition with other carnivores for prey. *Cougar: Ecology & Conservation* (eds M. Hornocker & S. Negri), pp. 163–172. University of Chicago Press, Chicago.

Rutishauser, M., Petkov, V., Boice, J., Obraczka, K., Mantey, P., Williams, T.M. & Wilmers, C.C. (2011) CARNIVORE : a disruption-tolerant system for studying wildlife. *EURASIP Journal on Wireless Communications and Networking*, **2011**, 1–14.

Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006) Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour*, **72**, 781–789.

Scantlebury, D.M., Mills, M.G.L., Wilson, R.P., Wilson, J.W., Mills, M.E.J., Durant, S.M., Bennett, N.C., Bradford, P., Marks, N.J. & Speakman, J.R. (2014) Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. *Science*, **346**, 79–81.

Scharf, A.K., Lapoint, S., Wikelski, M. & Safi, K. (2016) Acceleration data reveal highly individually structured energetic landscapes in free-ranging fishers (Pekania pennanti). *PlosOne*, **11**, e0145732.

Schmidt-Nielsen, K. (1972) Locomotion: Energy cost of swimming, flying, and running. *Science*, **177**, 222–228.

Schmidt-Nielsen, K. (1997) *Animal Physiology: Adaptation and Environment*, 5th ed. Cambridge University Press, New York.

Schmidt, K.P. & Gunson, J.R. (1985) Evaluation of wolf-ungulate predation near

Nordegg, Alberta. *Second Year Progress Report (1984-1985)*, p. Alberta Energy and Natural Resources Fish and Wildlife Division, Alberta.

Schmidt, K. & Kuijper, D.P.J. (2015) A "death trap" in the landscape of fear. *Mammal Research*, **60**, 275–285.

Schmidt, P.A. & Mech, L.D. (1997) Wolf pack size and food acquisition. *The American Naturalist*, **150**, 513–517.

Seebacher, F. & Franklin, C.E. (2012) Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **367**, 1607–14.

Seeherman, H.J., Taylor, C.R., Maloiy, G. & Armstrong, R.B. (1981) Design of the mammalian respiratory system II: Measuring maximum aerobic capacity. *Respiration Physiology*, **44**, 11–23.

Seidensticker, J.C., Hornocker, M.G., Wiles, W. V. & Messick, J.P. (1973) Mountain lion social organization in the Idaho Pimitive Area. *Wildlife Monographs*, 3–60.

Shahar, R. & Milgram, J. (2001) Morphometric and anatomic study of the hind limb of a dog. *American Journal of Veterinary Research*, **62**, 928–933.

Shamoun-Baranes, J., Bom, R., van Loon, E.E., Ens, B.J., Oosterbeek, K. & Bouten, W. (2012) From sensor data to animal behaviour: an oystercatcher example. *PloS one*, **7**, e37997.

Sheldon, C. (1930) *The Wilderness of Denali: Explorations of a Hunter-Naturalist in Northern Alaska*. Charles Scribner's Sons, New York.

Sheldon, J.W. (1992) *Wild Dogs: The Natural History of the Nondomesticated Canidae*. Academic Press, San Diego.

Shepard, E., Wilson, R., Halsey, L., Quintana, F., Gómez Laich, A., Gleiss, A., Liebsch, N., Myers, A. & Norman, B. (2008a) Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology*, **4**, 235–241.

Shepard, E., Wilson, R., Quintana, F., Gómez Laich, A., Liebsch, N., Albareda, D., Halsey, L., Gleiss, A., Morgan, D., Myers, A., Newman, C. & McDonald, D. (2008b) Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research*, **10**, 47–60.

Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S. a & Vosper, S.B. (2013) Energy landscapes shape animal movement ecology. *The American Naturalist*, **182**, 298–312.

Simberloff, D. (2003) How much information on population biology is needed to manage introduced species? *Conservation biology*, **17**, 83–92.

Skoglund, P., Ersmark, E., Palkopoulou, E. & Dalén, L. (2015) Ancient wolf genome reveals an early divergence of domestic dog ancestors and admixture into high-latitude breeds. *Current Biology*, **25**, 1515–1519.

Smith, J.B., Nielsen, C.K. & Hellgren, E.C. (2015a) Suitable habitat for recolonizing large carnivores in the midwestern USA. *Oryx*, **1**, 1–10.

Smith, J.A., Wang, Y. & Wilmers, C.C. (2015b) Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 1–6.

Smith, J.A., Wang, Y. & Wilmers, C.C. (2016) Spatial characteristics of residential development shift large carnivore prey habits. *The Journal of Wildlife Management*, **80**, 1040–1048.

Snow, D.H. (1985) The horse and dog, elite athletes—why and how? *Proceedings of the Nutrition Society*, **44**, 267–272.

Somero, G.N. (2011) Comparative physiology: a "crystal ball" for predicting consequences of global change. *American journal of physiology. Regulatory, integrative and comparative physiology*, **301**, R1–R14.

Speakman, J.R. (1997) *Doubly Labelled Water: Theory and Practice*. Chapman and Hall, London, United Kingdom.

Speakman, J.R. (2000) The Cost of Living: Field Metabolic Rates of Small Mammals. *Advances in Ecological Research*, pp. 177–297. Academic Press.

Speakman, J.R., Van Acker, A. & Harper, E.J. (2003) Age-related changes in the metabolism and body composition of three dog breeds and their relationship to life expectancy. *Aging Cell*, **2**, 265–275.

Spoor, C.F. & Badoux, D.M. (1988) Descriptive and functional myology of the back and hindlimb of the striped hyena (Hyaena hyaena, L. 1758). *Anatomischer Anzeiger*, **167**, 313–321.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ.

Steudel, K. (2000) The physiology and energetics of movement: effects on individuals and groups. *On the Move* (eds S. Boinski & P.. Garber), pp. 9–23.

University of Chicago Press, Chicago.

Tatner, P. & Bryant, D.M. (1986) Flight cost of a small passerine measured using doubly labeled water: Implications for energetics studies. *The Auk*, **103**, 169–180.

Taylor, M.E. (1989) Locomotor adaptations by carnivores. *Carnivore behavior, ecology and evolution* (ed J.L. Gittleman), pp. 382–409. Cornell University Press, Ithaca, NY.

Taylor, C.R. (1994) Relating mechanics and energetics during exercise. *Advances in Veterinary Science and Comparative Medicine*, **38A**, 181–215.

Taylor, C.R., Heglund, N.C. & Maloiy, G.M.. (1982) Energetics and mechanics of terrestrial locomotion 1. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology*, **97**, 1–21.

Taylor, C.R., Karas, R.H. & Weibel, E.R. (1987a) Adaptive variation in the mammalian respiratory system in relation to energetic demand II. Reaching the limits to oxygen flow. *Respiration Physiology*, **69**, 7–26.

Taylor, R., Maloiy, G., Weibel, E. & Al, E. (1980) Design of the mammalina respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respiration Physiology*, **44**, 25–37.

Taylor, C.R., Weibel, E.R. & Karas, R.H. (1987b) Adaptive variation in the mammalian respiratory system in relation to energetic demand VIII: Structural and functional design principles determining the limits to oxidative metabolism. *Respiration Physiology*, **69**, 117–127.

Terborgh, J. & Estes, J.A. (eds). (2010) *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śnieżko, S. & Gula, R. (2003) Daily patterns and duration of wolf activity in the Białowieża Forest, Poland. *Journal of Mammalogy*, **84**, 243–253.

Thompson, W.L. (ed). (2004) *Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters*. Island Press.

Thurber, J.M. & Peterson, R.O. (1993) Effects of Population Density and Pack Size on the Foraging Ecology of Gray Wolves. *Journal of Mammology*, **74**, 879–889.

Tollefson, C. (2013) Service Proposes to Return Management and Protection of Gray Wolves to State Wildlife Professionals Following Successful Recovery Efforts.

Tomlinson, S., Arnall, S.G., Munn, A., Bradshaw, S.D., Maloney, S.K., Dixon, K.W. & Didham, R.K. (2014) Applications and implications of ecological energetics. *Trends in ecology & evolution*, **29**, 1–11.

Torres, B.T., Moens, N.M.M., Al-Nadaf, S., Reynolds, L.R., Fu, Y.-C. & Budsberg, S.C. (2013) Comparison of overground and treadmill based gaits of dogs. *American Journal of Veterinary Research*, **74**, 535–541.

U.S. Fish & Wildlife Service. (2016) Gray wolves in the northern Rocky Mountains. URL https://www.fws.gov/mountain-prairie/es/grayWolf.php# [accessed 2 March 2017]

Udell, M. a R., Dorey, N.R. & Wynne, C.D.L. (2010) What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*,

85, 327–345.

Vanak, A.T., Dickman, C.R., Silva-Rodriguez, E.A., Butler, J.R.A. & Ritchie, E.G. (2013) Top-dogs and Under-dogs: Competition between Dogs and Sympatric Carnivores. *Free-Ranging Dogs and Wildlife Conservation* (ed M.E. Gompper), p. Oxford University Press.

Vaysse, A., Ratnakumar, A., Derrien, T., Axelsson, E., Rosengren Pielberg, G., Sigurdsson, S., Fall, T., Seppälä, E.H., Hansen, M.S.T., Lawley, C.T., Karlsson, E.K., Bannasch, D., Vilà, C., Lohi, H., Galibert, F., Fredholm, M., Häggström, J., Hedhammar, A., André, C., Lindblad-Toh, K., Hitte, C. & Webster, M.T. (2011) Identification of genomic regions associated with phenotypic variation between dog breeds using selection mapping. *PLoS Genetics*, **7**, e1002316.

Vonholdt, B.M., Pollinger, J.P., Lohmueller, K.E., Han, E., Parker, H.G., Quignon, P., Degenhardt, J.D., Boyko, A.R., Earl, D. a, Auton, A., Reynolds, A., Bryc, K., Brisbin, A., Knowles, J.C., Mosher, D.S., Spady, T.C., Elkahloun, A., Geffen, E., Pilot, M., Jedrzejewski, W., Greco, C., Randi, E., Bannasch, D., Wilton, A., Shearman, J., Musiani, M., Cargill, M., Jones, P.G., Qian, Z., Huang, W., Ding, Z.-L., Zhang, Y.-P., Bustamante, C.D., Ostrander, E. a, Novembre, J. & Wayne, R.K. (2010) Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature*, **464**, 898–902.

Vucetich, J.A., Peterson, R.O. & Waite, T.A. (2004) Raven scavenging favours group foraging in wolves. *Animal Behaviour*, **67**, 1117–1126.

Vander Waal, S.B. (1990) *Food Hoarding in Animals*. University of Chicago Press,

Chicago.

Wang, Y., Allen, M.L. & Wilmers, C.C. (2015a) Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation*, **190**, 23–33.

Wang, Y., Nickel, B., Rutishauser, M., Bryce, C.M., Williams, T.M., Elkaim, G. & Wilmers, C.C. (2015b) Movement, resting, and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements. *Movement Ecology*, **3**, 1–12.

Wang, G.D., Zhai, W., Yang, H.C., Fan, R.X., Cao, X., Zhong, L., Wang, L., Liu, F., Wu, H., Cheng, L.G., Poyarkov, a D., Poyarkov Jr., N. a, Tang, S.S., Zhao, W.M., Gao, Y., Lv, X.M., Irwin, D.M., Savolainen, P., Wu, C.I. & Zhang, Y.P. (2013) The genomics of selection in dogs and the parallel evolution between dogs and humans. *Nature Communications*, **4**, 1860.

Wang, G.-D., Zhai, W., Yang, H.-C., Wang, L., Zhong, L., Liu, Y.-H., Fan, R.-X., Yin, T.-T., Zhu, C.-L., Poyarkov, A.D., Irwin, D.M., Hytönen, M.K., Lohi, H., Wu, C.-I., Savolainen, P. & Zhang, Y.-P. (2016) Out of southern East Asia: the natural history of domestic dogs across the world. *Cell Research*, **26**, 21–33.

Warrick, D.R. (1998) The turning- and linear-maneuvering performance of birds: the cost of efficiency for coursing insectivores. *Canadian Journal of Zoology*, **76**, 1063–1079.

Wayne, R.K. (1986) Limb morphology of domestic and wild canids: The influence of development on morphologic change. *Journal of Morphology*, **187**, 301–319.

Wayne, R.K. (2001) Consequences of domestication: morphological diversity of the dog. *The Genetics of the Dog* (eds A. Ruvinksy & J. Sampson), pp. 43–60. CABI Publishing, Oxon, UK.

Weibel, E.R., Bacigalupe, L.D., Schmitt, B. & Hoppeler, H. (2004) Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as determinant factor. *Respiratory Physiology & Neurobiology*, **140**, 115–32.

Weibel, E.R. & Hoppeler, H. (2005) Exercise-induced maximal metabolic rate scales with muscle aerobic capacity. *The Journal of Experimental Biology*, **208**, 1635–44.

Weibel, E.R., Taylor, C.R., Neil, J.J.O., Leith, D.E., Gehr, P., Hoppeler, H., Langman, V.A.U.G.H.A.N. & Baudinette, R. V. (1983) Maximal oxygen consumption and pulmonary diffusing capacity: A direct comparison of physiological and morphometric measurements in canids. *Respiration Physiology*, **54**, 173–188.

Weibel, E.R., Taylor, C.R. & Richard, H. (1987) Adaptive variation in the mammalian respiratory system in relation to energetic demand I: Introduction to problem and strategy. *Respiration Physiology*, **69**, 1–6.

Weiner, J. (1989) Metabolic constraints to mammalian energy budgets. *Acta Theriologica*, **34**, 3–35.

Wentink, G.H. (1979) Dynamics of the hind limb at walk in horse and dog. *Anatomy and Embryology*, **155**, 179–190.

Western Regional Climate Center. (2016) McKinley Park, Alaska: period of record

monthly climate summary. URL http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak5778

Westerterp, K., Saris, W., Van Es, M. & Hoor, F. ten. (1986) Use of the doubly labeled water technique in humans during heavy sustained exercise. *Journal of Applied Physiology*, **61**, 2161–2167.

Whittington, J., St. Clair, C.C. & Mercer, G. (2005) Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications*, **15**, 543–553.

Wierzbowska, I.A., Hędrzak, M., Popczyk, B., Okarma, H. & Crooks, K.R. (2016) Predation of wildlife by free-ranging domestic dogs in Polish hunting grounds and potential competition with the grey wolf. *Biological Conservation*, **201**, 1–9.

Wikelski, M. & Cooke, S.J. (2006) Conservation physiology. *Trends in Ecology & Evolution*, **21**, 38–46.

Wilcox, B. & Walkowicz, C. (1995) *Atlas of Dog Breeds of the World*, 5th edn. T.F.H. Publications, Neptune City, NJ.

Williams, T.M. (1999) The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **354**, 193–201.

Williams, C.T., Barnes, B.M. & Buck, C.L. (2016) Integrating physiology, behavior, and energetics: Biologging in a free-living arctic hibernator. *Comparative Biochemistry and Physiology -Part A: Molecular and Integrative Physiology*, **202**, 53–62.

Williams, T.M., Ben-David, M., Noren, S., Rutishauser, M., McDonald, K. &

Heyward, W. (2002) Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land? *Comparative biochemistry and physiology. Part A, Molecular & integrative physiology*, **133**, 203–12.

Williams, T.M., Bengtson, P., Steller, D.L., Croll, D.A. & Davis, R.W. (2015) The healthy heart: Lessons from nature's elite athletes. *Physiology*, **30**, 349–357.

Williams, T.M., Fuiman, L.A., Horning, M. & Davis, R.W. (2004) The cost of foraging by a marine predator, the Weddell seal Leptonychotes weddellii: pricing by the stroke. *Journal of Experimental Biology*, **207**, 973–982.

Williams, J.S., McCarthy, J.J. & Picton, H.D. (1995) Cougar habitat use and food habits on the Montana Rocky Mountain front. *Intermountain Journal of Science*, **1**, 16–28.

Williams, S.B., Wilson, A.M., Rhodes, L., Andrews, J. & Payne, R.C. (2008) Functional anatomy and muscle moment arms of the pelvic limb of an elite sprinting athlete: The racing greyhound (Canis familiaris). *Journal of Anatomy*, **213**, 361–372.

Williams, T.M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G.H. & Wilmers, C.C. (2014) Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science*, **346**, 81–85.

Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M. & Getz, W.M. (2003) Facilitation by introduced trophic top predators: grey wolf in Yellowstone National Park subsidies to scavengers. *Journal of Animal Ecology*, **72**, 909–916.

Wilmers, C.C., Nickel, B., Bryce, C.M., Smith, J.A., Wheat, R.E. & Yovovich, V.

(2015) The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*, **96**, 1741–1753.

Wilmers, C.C., Post, E. & Hastings, A. (2007) The anatomy of predator-prey dynamics in a changing climate. *The Journal of Animal Ecology*, **76**, 1037–44.

Wilmers, C.C., Post, E., Peterson, R.O. & Vucetich, J.A. (2006) Predator disease outbreak modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters*, **9**, 383–389.

Wilmers, C.C. & Schmitz, O.J. (2016) Effects of gray wolf-induced trophic cascades on ecosystem carbon cycling. *Ecosphere*, **7**, 1–10.

Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V. & Williams, T. (2013) Scale dependent behavioral responses to human development by a large predator, the puma. *PloS one*, **8**, e60590.

Wilson, A.M., van den Borget, A.J. & McGuigan, M.P. (2000) Optimization of the muscle-tendon unit for economical locomotion in cursorial animals. *Skeletal Muscle Mechanics: From Mechanisms to Function* (ed W. Herzog), pp. 517–547. Wiley, New York.

Wilson, R.P., Griffiths, I.W., Legg, P. a, Friswell, M.I., Bidder, O.R., Halsey, L.G., Lambertucci, S. a & Shepard, E.L.C. (2013a) Turn costs change the value of animal search paths. *Ecology letters*, **16**, 1145–50.

Wilson, R.P., Griffiths, I.W., Mills, M.G., Carbone, C., Wilson, J.W. & Scantlebury, D.M. (2015) Mass enhances speed but diminishes turn capacity in terrestrial

pursuit predators. *eLife*, **4**, 1–18.

Wilson, A.M., Lowe, J.C., Roskilly, K., Hudson, P.E., Golabek, K. a. & McNutt, J.W. (2013b) Locomotion dynamics of hunting in wild cheetahs. *Nature*, **498**, 185–189.

Wilson, a M., McGuigan, M.P., Su, a & van Den Bogert, a J. (2001) Horses damp the spring in their step. *Nature*, **414**, 895–899.

Wilson, J.W., Mills, M.G.L., Wilson, R.P., Peters, G., Mills, M.E.J., John, R., Durant, S.M., Bennett, N.C., Marks, N.J., Scantlebury, M. & Speakman, J.R. (2013c) Cheetahs, Acinonyx jubatus, balance turn capacity with pace when chasing prey. *Biology Letters*, **9**, 2–6.

Wilson, R.P., Quintana, F. & Hobson, V.J. (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 975–80.

Wilson, R., Shepard, E.L.C. & Liebsch, N. (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research*, **4**, 123–137.

Wilson, R.P., White, C.R., Quintana, F., Halsey, L.G., Liebsch, N., Martin, G.R. & Butler, P.J. (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *The Journal of Animal Ecology*, **75**, 1081–90.

Withers, C. (1977) Measurement of VO2, VCO2, and evaporative water loss with a flow-through mask. *Journal of Applied Physiology*, **42**, 120–123.

Withers, P.C., Cooper, C.E., Maloney, S.K., Bozinovic, F. & Cruz-Neto, A.P. (2016a) Physiological Characteristics of Mammals. *Ecological and Environmental Physiology of Mammals* (eds P.C. Withers, C.E. Cooper, S.K. Maloney, F. Bozinovic & A.P. Cruz-Neto), pp. 146–289. Oxford University Press, Oxford.

Withers, P.C., Cooper, C.E., Maloney, S.K., Bozinovic, F. & Cruz-Neto, A.P. (eds). (2016b) *Ecological and Environmental Physiology of Mammals*. Oxford University Press, Oxon, UK.

Wong, B.B.M. & Candolin, U. (2014) Behavioral responses to changing environments. *Behavioral Ecology*, 1–9.

Wright, B.M., Ford, J.K.B., Ellis, G.M., Deecke, V.B., Shapiro, A.D., Battaile, B.C. & Trites, A.W. (2017) Fine-scale foraging movements by fish-eating killer whales (Orcinus orca) relate to the vertical distributions and escape responses of salmonid prey (Oncorhynchus spp.). *Movement Ecology*, **5**, 1–18.

Young, S.P. (1946) History, life habits, economic status, and control, Park 1. *The Puma: Mysterious American Cat* (eds S.P. Young & E.A. Goldman), pp. 1–173. Washington, DC.