Mammalian Biology 86 (2017) 66–69

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Short communication

Attraction-repulsion among top predators following reintroduction efforts

L. Mark Elbroch[a], Carlos López-González[b,*], Jenny Fitzgerald[a], Anna Kusler[a], Howard Quigley[a]

[a] Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, United States
[b] Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, Mexico

ARTICLE INFO

Article history:
Received 18 October 2016
Accepted 20 April 2017
Handled by Francesco Ferretti
Available online 26 April 2017

Keywords:
Animal movement
Competition
Interactions
MoveMine 2.0

ABSTRACT

Much of our understanding of the effects top predators play in structuring ecological communities are from studies documenting ecological changes following the recovery or reintroduction of large carnivores. Reintroduced predators, for example, may create unanticipated competition scenarios that influence local carnivore guilds. Here, we tested whether newly released Mexican gray wolves in Chihuahua, Mexico interacted with resident pumas, as a first step in exploring potential competition between the two species. We employed GPS data and novel methods offered by MoveMine 2.0 to quantify attraction-repulsion between individual wolves and pumas during two time periods: the first when wolves were free roaming, and the second when they restricted their movements to an area around their den and rendezvous site to protect and provide for pups. In summary, attraction-repulsion analyses conducted with MoveMine provided meaningful outputs, but we would highlight the importance of fieldwork to interpret interactions and significance values calculated between pairs. We found that high attraction values resulted from mutual attraction between wolves in the same pack, between wolves and one puma they repeatedly harassed, as well as between two pumas that repeatedly exhibited social tolerance for each other. Thus, the analyses offered by MoveMine provided a powerful means of identifying interactions and assessing attraction-repulsion relevant to questions of intra- and interspecific competition, but required intimate knowledge of the species studied and the interactions between them to interpret outputs correctly.

Large carnivores demand significant research interest and resources due to their keystone ecological functions in natural systems, their reliance on conservation strategies for persistence, and their controversial roles as competitors with humans for prey species and livestock (Ordiz et al., 2013; Ripple et al., 2014). Tolerance for large carnivores has also increased across Europe and North America (Chapron et al., 2014), providing opportunities for reintroduction efforts to enhance local biodiversity and increase ecological resilience (Seddon et al., 2007). Such reintroductions have created natural experiments that have dramatically increased our understanding of the positive roles top predators play in structuring ecological communities (e.g., Ripple and Beschta, 2011). Reintroduced predator populations also create sometimes-unanticipated competition scenarios that influence local carnivore guilds. For example, reintroduced top predators may change the abundance or fitness of subordinate predators (e.g., Harihar et al., 2011; Levi and Wilmers, 2012; Roemer et al., 2002), as well as influence a subordinate predator's access to important resources (e.g., prey) through interference or exploitation competition (e.g., Elbroch et al., 2015; Harihar et al., 2011; Lendrum et al., 2014).

Ecosystem changes following gray wolf (*Canis lupus*) reintroductions in Yellowstone National Park, USA, have been researched intensively and resulted in a rich scientific literature on the direct and indirect effects of wolves on prey, their competitors, the spatial distribution of predation risk, and trophic cascades influencing lower trophic communities (e.g., Kauffman et al., 2007; Ripple and Beschta, 2011; Vucetich et al., 2005). In contrast, little research on the ecological consequences of the reintroduction of Mexican gray wolves (*C. l. baileyi*) in eastern Arizona in 1998 has been published. Mexican gray wolves were widespread in the southwest United States and northwest Mexico, however heavy persecution by settlers in both the USA and Mexico led to their near extinction by 1970. In 1976, the United States Fish and Wildlife Service declared Mexican wolves an endangered species, and subsequently created a joint US-Mexico captive breeding program with five wolves cap-

* Corresponding author at: Cerro de Las Campanas, s/n, Las Campanas, 76010 Santiago de Querétaro, QRO, Mexico.
E-mail address: cats4mex@gmail.com (C. López-González).

http://dx.doi.org/10.1016/j.mambio.2017.04.003
1616-5047/

tured in northern Mexico from 1977 to 1980. On March 29, 1998, the first 11 captive-bred wolves were released in the southwestern United States, where today they number 97 wild wolves (USFW, 2017).

Since the start of the release program, the recovery of Mexican gray wolves was mired in political and management obstacles (Povilitis et al., 2006), limiting research opportunities. Nevertheless, the reintroduction efforts of Mexican gray wolves expanded beyond the United States to northern Mexico in 2012, following initial ecological assessments and public interviews (Rodriguez et al., 2003; SEMARNAT, 2000). Here, we tested whether newly released Mexican gray wolves in Chihuahua, Mexico interacted with resident pumas, as a first step in exploring potential competition between the two species. The local puma population was not monitored previous to the release of wolves, but pumas were known to exist in the area from interviews with local ranchers. Like wolves, pumas suffered persecution, but they likely survived at low densities in the study area in the absence of Mexican wolves for 50 years or more.

We employed GPS data, and a novel method and software (MoveMine 2.0; Li et al., 2014) to assess attraction-repulsion between individual wolves and pumas. We hypothesized that new wolves would be attracted to pumas because of opportunities to kleptoparasitize puma kills while they learned their area and increased their own hunting efficiency (e.g., Bartnick et al., 2013; Kunkel et al., 1999). Alternatively, during the denning season, we predicted that wolves would repel pumas because of the need to protect their pups from predation. We conducted our research in northern Mexico, on private cattle ranches that cannot be disclosed due to the sensitivity of wolf reintroductions. The study area spanned approximately 440 km^2 of the Sierra Madre Mountains, with marked wolves and pumas sometimes moving outside these limits. Elevations in the study area ranged from 1600 m–2600 m above sea level and the terrain was characterized by rugged canyons and rock pillars. Temperatures ranged from 0 °C–31 °C over the year, with intermittent snowfall during winter, and monsoon rains from June-October; annual precipitation was 450–550 mm (Villanueva-Diaz et al., 2007). The vegetation cover was predominantly open oak (*Quercus* spp.) forest (57.75% of the study area), which was characterized by vast open grasslands with dispersed trees. Other cover classes included secondary vegetation (36.77%), defined as a mix of many species (oak, *Quercus* spp., pine, *Pinus* spp., madrone, *Arbutus* spp., Mexican manzanita, *Arctostaphylos pungens*, yucca, *Yucca filifera*, sotol *Dasylirion acrotriche*), oak-pine forest (5.35%), and pine forest (0.17%). In the dry months, water was limited to perennial springs and creeks, as well as man-made holding tanks for livestock.

Wolves were captive bred in the USA and a male-female pair was released in Chihuahua in 2012 wearing Vectronics GPS Globalstar Plus collars that obtained location data at 2-h intervals (12 times/day). Two pups born in the wild were caught with padded leg hold traps and fitted with the same collar system. Four pumas were caught using foot snares (Logan et al., 1999). Snares were monitored every 1–1.5 h during the night via telemetry devices that relayed when they had been tripped, and three times per day during daylight hours. Pumas were marked with Vectronics GPS Plus and Vertrex collars, which obtained location data every two hours (12 times/day). Capture and handling methods were reviewed and approved under permits SGPA/DGVS/13782/14, SGPA/DGVS/06705/16, and SGPA/DGVS/00340/16.

We employed permutation tests in MoveMine software (Li et al., 2014) to determine whether two moving objects met more (attraction) or less (repulsion) than expected by chance given their spatial overlap and simultaneous trajectories. MoveMine requires GPS data and for users to input distance and time parameters to define spatial interactions between individual objects or animals. Following published literature (Elbroch and Quigley, 2016), we used 200 m as the threshold distance between animals that would be classified as an interaction, and 1 h as the time threshold for the animals to have been within 200 m of each other, because some collars acquired location data at odd hours from each other. The attraction-repulsion analysis calculated an output spectrum ranging from 0 to 1 based upon the frequency of interactions and GPS trajectories of marked individuals, where 0 was absolute repulsion and 1 was absolute attraction (mathematical details are found in Li et al., 2014). We divided the analysis into two time periods: December 15, 2015–April 19, 2016, during which wolves were moving freely about their territory, and April 20, 2016–July 30, 2016, when the wolves were in an active den and utilizing a rendezvous site where pups remained while adults were hunting. We split the analysis this way because we expected that wolf defensive behaviors associated with new pups might influence attraction-repulsion between wolves and pumas. Marked pumas did not exhibit ay changes in parental status across both time periods. We tested for a difference in mean puma-wolf attraction values across time periods using a paired *t*-test.

For our analysis, we included three pumas and three wolves that overlapped in space and time: P1 was a resident male puma, P3 was an adult female puma with two kittens of approximately 7 months, P4 was an adult female puma without kittens. M1215 was a reintroduced male wolf, and alpha of the pack. At this time, he is the only male to have reproduced in the wild since reintroduction efforts began. F1449 was a subadult female wolf born in the wild in spring 2014, and F1448 was a subadult female wolf born in the wild in spring 2015. We included three members of the same pack in the analysis for two reasons: 1) the mean distance between wolves at 500 random times we obtained simultaneous locations was greater than our interaction threshold of 200 m (F1448- F1449, $\overline{X} = 874.9 \pm 77.4$ m; M1215–F1449, $\overline{X} = 994.3 \pm 79.3$ m; M1215-F1448, $\overline{X} = 963.2 \pm 76.3$ m), and 2) the inclusion of all three wolves allowed us to assess software performance, as we assumed results for attraction between them would be close to 1 given that they were social animals in the same pack. Such findings would provide support for results between pumas and wolves.

During both time periods, the three wolves showed absolute attraction for each other, as expected for members of the same pack. From December 15, 2015–April 19, 2016, two pumas (P3, P4) exhibited attraction with the three wolves, whereas P1 exhibited repulsion with the three wolves. We were able to verify an instance where P4 took refuge in a tree to escape the three wolves; all four animals remained in place for 6 h. In another exchange, we verified that P4 was chased off a carcass by the wolves. P1 exhibited repulsion with the other two pumas, whereas P3 and P4 exhibited attraction between them. In one instance we were able to verify that P4 had killed a deer, and tolerated P3 feeding at the carcass as well.

From April 20, 2016–July 30, 2016, one puma (P1) exhibited absolute attraction with the three wolves, a second puma (P3) exhibited slight attraction for the three wolves, and the third puma (P4) exhibited repulsion with the three wolves. P3 and P4 spent 12 h together on one occasion, and exhibited strong attraction between them. The other puma pairings exhibited repulsion, as might be expected for a territorial species. The number of interactions and attraction values for all dyads can be found in Fig. 1. We did not find a difference in attraction significance values from one time period to the next ($t_8 = 0.18$, P = 0.86).

In summary, our attraction-repulsion analysis provided meaningful outputs and tools for researchers interested in intra- and interspecific social organization, competition, avoidance, or even habituation in animals. For example, an analysis of