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# Tolerance of wolves shapes desert canid communities in the Middle East

Gavin T. Bonsen[a,*], Arian D. Wallach[a], Dror Ben-Ami[b], Oded Keynan[b,c], Anton Khalilieh[d], Uri Shanas[e], Eamonn I.F. Wooster[a], Daniel Ramp[a]

[a] *Centre for Compassionate Conservation, Faculty of Science, University of Technology Sydney, New South Wales 2007, Australia*
[b] *Compassionate Conservation Middle East, Steinhardt Museum of Natural History, Tel Aviv University, Israel*
[c] *Dead Sea and Arava Science Centre, Central Arava Branch, Hazeva, Israel*
[d] *Nature Palestine Society, Ramallah, Palestine*
[e] *Biology and Environment, University of Haifa – Oranim, Tivon, Israel*

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ABSTRACT

The grey wolf (*Canis lupus*) is recovering globally due to increasing human acceptance, which can drive trophic cascades. An endangered subspecies, the Arabian wolf (*Canis lupus arabs*), inhabits arid regions of the southern Levant and Arabian Peninsula where it remains widely persecuted, and little is known about its ecology. Most of the Arabian wolf's range is dominated by pastoralism, where tolerance of wolves is low. We assessed how acceptance of Arabian wolves, relative to human land-use and density, has cascading effects on other canids by comparing spatial and temporal interactions, and relative abundance of canids across a hyper-arid desert crossing the Israel-Jordan border. Canids responded by adjusting their spatial and temporal activity patterns in relation to human activity. Wolves were recorded significantly less in pastoralist landscapes, leading to cascading effects. We found that jackals (*Canis aureus*) and foxes (*Vulpes* spp.) are both suppressed by larger canids. Wolves and jackals both suppressed foxes, but wolves also facilitated foxes by reducing pressure from jackals. Representing the first documentation of the role of an apex predator in the Middle East, our findings highlight the strong ecological effects that Arabian wolves have on desert ecosystems. Conservation efforts should focus on increasing tolerance and working towards coexistence in pastoralist landscapes.

## 1. Introduction

The grey wolf (*Canis lupus*) is recovering across its global range, particularly in North America and Europe, largely due to a general increase in human acceptance of predators (George et al., 2016) and the transition of some farming regions to wild spaces (Chapron et al., 2014). The ecological implications of this recovery have been demonstrated in some protected areas like Yellowstone National Park, USA (Ripple and Beschta, 2011). However, persecution remains the greatest threat to large predators globally, including wolves (Ripple et al., 2014). Animal production, specifically of free-ranging domestic ungulates (i.e., pastoralism), remains one of the main

* Corresponding author.
*E-mail addresses:* Gavin.Bonsen@uts.edu.au (G.T. Bonsen), Arian.Wallach@uts.edu.au (A.D. Wallach), drorbe@post.tau.ac.il (D. Ben-Ami), oded@adssc.org (O. Keynan), anton.sunbird@gmail.com (A. Khalilieh), shanas@research.haifa.ac.il (U. Shanas), Eamonn.Wooster@uts.edu.au (E.I.F. Wooster), Daniel.Ramp@uts.edu.au (D. Ramp).

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drivers of predator persecution (Boronyak et al., 2020). Wolf-induced trophic cascades have gained much attention in areas where populations are recovering, but the removal of apex predators also triggers cascades (Colman et al., 2014; Heath et al., 2014). While the recovery and ecological effects of wolves in North America and Europe are well understood, less is known about the ecological roles of wolves in other regions.

The desert-adapted Arabian wolf (*C. l. arabs*), the smallest subspecies of grey wolf, was historically widespread across arid regions of the southern Levant and Arabian Peninsula, but it is now endangered due to persecution (Mallon and Budd, 2011). The Arabian wolf remains the sole apex predator across most of its range since the extirpation of the Asiatic cheetah (*Acinonyx jubatus venaticus*) and the near-eradication of the Arabian leopard (*Panthera pardus nimr*) during the last several decades. Elucidating the important ecological roles of Arabian wolves is likely to enhance the conservation of this endangered grey wolf subspecies (Sakurai et al., 2020). The only known stable population is confined to the Arava Valley and Negev Desert in Israel, where legal protection is enforced and acceptance of wolves is high (Barocas et al., 2018; Cohen et al., 2013). Wolves in this region also benefit from the legal protection of their prey, such as gazelle (*Gazella* spp.), and from water and food (e.g., dates and melons) resources available at crop farms (Barocas et al., 2018; Lewin et al., 2021). However, most of the Arabian wolf's range overlaps with semi-nomadic sheep and goat herders, and like most regions where pastoralism occurs, predators are killed to protect domestic animals from predation. The question remains whether Arabian wolves structure ecosystems in similar ways to their northern counterparts.

As apex predators, wolves are known to suppress populations of smaller canids in other parts of the world. In North America, wolves limit the distribution and abundance of coyotes (*C. latrans*) (Berger and Gese, 2007), while the ranges and densities of wolves and golden jackals (*C. aureus*) are negatively correlated in Europe (Krofel et al., 2017; Newsome et al., 2017). Likewise, across the deserts of Australia, the closely-related dingo (*C. dingo*) has strong suppressive effects on red foxes (*Vulpes vulpes*) (Wallach et al., 2010; Wooster et al., 2021). The suppressive effects of large canids can cascade through the predator community. For example, the suppression of coyotes by wolves has released red foxes (Levi and Wilmers, 2012; Newsome and Ripple, 2015). In core agricultural areas of Israel, foxes avoid areas of high jackal density (Shamoon et al., 2017), and foxes also avoid jackals at fine spatial scales in agricultural landscapes of the Arava Valley (Scheinin et al., 2006). Humans influence canid communities through both agonistic and facilitative interactions in the Middle East. Wolves remain heavily persecuted in pastoralist landscapes on the Arabian Peninsula (Cunningham et al., 2009). In the southern Levant, golden jackals have expanded their range into arid regions along with agricultural development (Magory Cohen et al., 2013), and are often culled due to perceived economic impacts to agriculture and the spread of rabies (Nemtzov

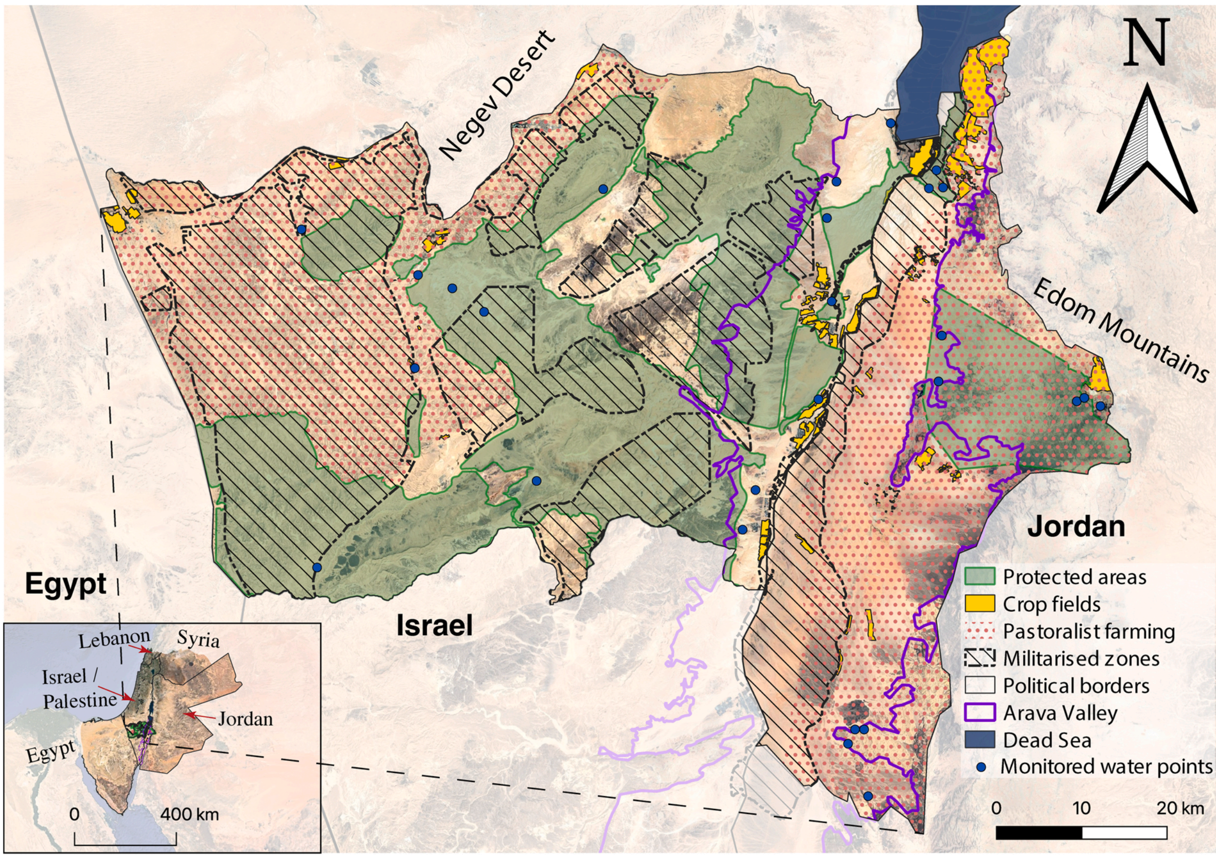


**Fig. 1.** Spatial distribution of monitored water points across three human land-use categories within a ~6000 km$^2$ study area in the southern Levant (inset), highlighting the Arava Valley (outlined in purple) which straddles the international border between Israel and Jordan.

and King, 2001). Here, we ask whether contrasting human attitudes shape the cascading ecological effects that Arabian wolves may have on mesopredators. We hypothesised that when humans are tolerant of wolves, the ecological effects of wolves will be stronger than when humans persecute wolves.

To test this hypothesis, we assessed spatial and temporal interactions of Arabian wolves, golden jackals, and foxes between different human contexts based on human acceptance of wolves, with an aim to determine if acceptance of wolves shaped canid communities in a Middle Eastern hyper-arid desert. We quantified spatial and temporal avoidance of smaller canids toward larger canids across protected areas and agricultural landscapes dominated by either pastoralism or crop farming. Given that tolerance of wolves is low in pastoralist landscapes, we predicted a reduction in wolf activity, releasing jackals from top-down pressure and cascading to intensify suppression of foxes.

## 2. Materials and methods

### 2.1. Study area

We measured canid activity patterns across a ~6000 km$^2$ region of desert in the southern Levant (Fig. 1) during the summer (June-September) of 2019. Almost all rainfall in this arid to hyper-arid region (e.g., < 50 mm in lowland, < 200 mm in highland areas) occurs within 6-month periods surrounding winter (October to March). Temperatures reach > 45°C in summer (< 10°C cooler in the highlands), so the study area was typically dry and hot during sampling. Our study area incorporated both highland and lowland areas, stretching across the Negev Desert from the Israel-Egypt border in the west (highest peak ~1000 m) to Jordan's Edom Mountains in the east (highest peak ~1200 m). Bisecting these two highland areas is the hyper-arid Arava Valley (Arabic: وادي عربة, 'Wadi Araba'; Hebrew: עֲרָבָה 'Arava'), which straddles the Israel-Jordan border, and its lowest point reaches 400 m below sea level at the southern shore of the Dead Sea. Our study area covered the northern section of the Arava Valley (spanning 50–70 km south of the Dead Sea), encompassing a contiguous lowland desert ecosystem averaging 20 km wide, and its adjacent arid highlands to the east and west.

The southern Levant is a socio-politically complex region encompassing parts of Israel, Palestine, and Jordan, where acceptance of wolves varies. The Arabian wolf is legally protected throughout the region, but protection is only enforced in limited areas and community support for predator protection in pastoralist landscapes is generally low. Arabian wolves have reportedly been shot after crossing into pastoralist landscapes in the past (Hefner and Geffen, 1999). Legal and illegal hunting is common in some pastoralist landscapes (Eid and Handal, 2018), and several threatened species, including the Arabian wolf (Bonsen and Khalilieh, 2021), can be confined to nature reserves (Amr et al., 2004). A severely depleted wild prey base outside of protected areas means that domestic ungulates (hence 'livestock') are now an important food source for wolves in some pastoralist landscapes (Bonsen and Khalilieh, 2021), often exacerbating conflicts (Gecchele et al., 2017). In crop farming landscapes absent of pastoralism, tolerance of wolves is high (Barocas et al., 2018), which expands the areas of protection for wolves.

The section of the Israel-Jordan border running through our study area had no physical barrier. Simple barbed-wire fences enclosing minefields along the Israeli side of the border are remnants of times before the ratification of the 1994 peace treaty. Unlike wildlife that can cross the border freely, human movement is controlled by the military on both sides. Within our study site, military activity in Jordan was concentrated predominantly within 5 km of the border, while Israel's military activity spanned the borders from Jordan to Egypt. The Negev contains extensive military training areas that are off limit to the public (including to pastoralists) apart from Saturdays and Jewish holidays when they are open for hiking and camping.

Thus, pastoralism is more restricted in Israel compared to Jordan where pastoralists are granted considerably more freedom in their movement and temporary settlement when herding. In Jordan, herders are allowed to bring their domestic sheep and goats into protected areas to drink at springs, whereas in Israel, livestock are excluded from protected areas. Within this part of Israel, most livestock are confined to dairy factory farms, and the small agricultural villages ('moshavim' and 'kibbutzim') are surrounded by intensive crop fields. Common crops include dates and seasonal cultivars such as melons and peppers, which form a considerable part of the diets of the region's canids (Lewin et al., 2021).

### 2.2. Data collection and analysis

We used data obtained from various sources to generate GIS layers in ArcGIS 10.8 (ESRI, 2019) based on human land-use and population density (see Table A1 in Supporting Information). We then characterised the study area into the three following categories based on land-use. (1) *Protected areas*: National parks and nature reserves primarily used for benign recreational activities, in which wildlife are legally and actively protected. The risk of wolf persecution is low. (2) *Crop farming landscapes*: Agricultural landscapes where crop farming is the main land-use, and large vertebrate wildlife are legally and actively protected. The risk of wolf persecution is similarly low to protected areas, but human activity is higher. (3) *Pastoralist landscapes*: Agricultural landscapes in which livestock herding is a predominant form of agriculture. Wolves are perceived as a threat to livestock (Barocas et al., 2018) and are illegally persecuted in some areas (Eid and Handal, 2018; Hefner and Geffen, 1999).

We set up 1–3 Trophy Cam Aggressor no-glow camera-traps (Bushnell, Overland Park, KS, USA) at 27 water points (natural springs, leaky pipes, artificial dams, and troughs) – nine in each land-use category – for approximately one month to estimate use, as well as spatial and temporal interactions, of canids across human contexts (Fig. 1). We focused on water points because this is where wildlife activity is highest, and where canids scent mark regularly (Wallach et al., 2009). We categorised the water point to land-use by determining the predominant human activity, and calculated the mean human population density, within a 5 km radius. Camera-trap data were sorted into species (for *Canis* spp.) or genus (for *Vulpes* spp.). The red fox (*V. vulpes*) was the most frequently detected fox species, but we combined their detections with two other foxes (*V. cana* and *V. rueppellii*) as they constitute a similar trophic position (all weigh $< 5$ kg).

We conducted single-species and two-species occupancy models using the package 'Wiqid' in program R version 4.0.1 (R Core Team, 2018). Given that water point availability was limited, and individual canid home ranges often consisted of multiple water points, we interpreted the occupancy parameter ($\psi$) from the single-species models as the probability of resource use to accommodate the lack of spatial independence (Mackenzie, 2006). We calculated a Species Interaction Factor (SIF) from the two-species models according to the equation proposed by Richmond et al. (2010). The SIF indicated whether a smaller canid avoided (SIF $< 1.0$) or was attracted to (SIF $> 1.0$) a larger canid, or if the two canids occurred independently (SIF $= 1.0$); the further the value is from the neutral value of 1.0, the stronger the interaction. The probability of resource use was modelled as a function of human population density within each land-use category, whereas a single SIF was calculated across the study area for each species pair.

We further explored interactions between canids by determining overlap in temporal activity patterns. We treated detection 'events' as independent if there were no other detections of the same canid for five minutes before or after the given event, and recorded the location, date, and time of each independent event. Using the 'overlap' package in R (Meredith and Ridout, 2020), we then estimated temporal activity patterns and fitted kernel density curves in radians ($r$). A coefficient of overlap ($\widehat{\Delta}$) was calculated as the area lying under the overlap in density curves for each canid, returning a value ranging from 0 (no overlap) to 1 (complete overlap). Following the recommendations of Ridout and Linkie (2009), we used $\widehat{\Delta}_1$ for small sample sizes ($< 75$) and $\widehat{\Delta}_4$ for large sample sizes ($>$ 75), and generated 1000 smoothed bootstrap samples; estimating a mean $\widehat{\Delta}$ and 95% confidence intervals (CI; *as per* Meredith and Ridout, 2020) for each pair of density curves within each land-use category. Finally, we tested for any significant change in temporal activity patterns for a given canid between land-use categories using a Wald's Test in the 'activity' package in R. Temporal activity patterns of humans were also analysed using camera-trap detections to visualise temporal adjustments in wolf activity in response to humans. We used package 'camtrapR' in R to define detection events and create detection histories used in occupancy models.

We also conducted tracking surveys to estimate an index of relative abundance of canids between the two agricultural land-use categories. We concentrated efforts in the Arava Valley to draw direct comparisons between crop farming and pastoralist landscapes across the Israel-Jordan border, while reducing confounding spatial factors such as differences in elevation or accessibility to prey or resources. Protected areas are small in the Arava and largely influenced by the surrounding agricultural activities, so sampling conducted within protected areas was classified according to the corresponding agricultural activity. Thus, for relative abundance estimates, all sampling units in crop farming landscapes were in Israel, while all sampling units in pastoralist landscapes were in Jordan.

Following Wallach et al. (2010), we used two different tracking methods to assess two parameters for each species: relative density and relative distribution. We then multiplied these two parameters together to obtain an index of relative abundance [$IR_{ab} = R_{dens}$ x $R_{dist}$], which we compared across land-use categories by performing a Kruskal-Wallis test for each species. To determine relative density, we counted the number of fresh tracks along 500 m transects (21 in crop farming, 17 in pastoralist areas) across an average of three consecutive mornings. After counting, we cleared any previously deposited tracks by dragging a heavy metal object, with dried

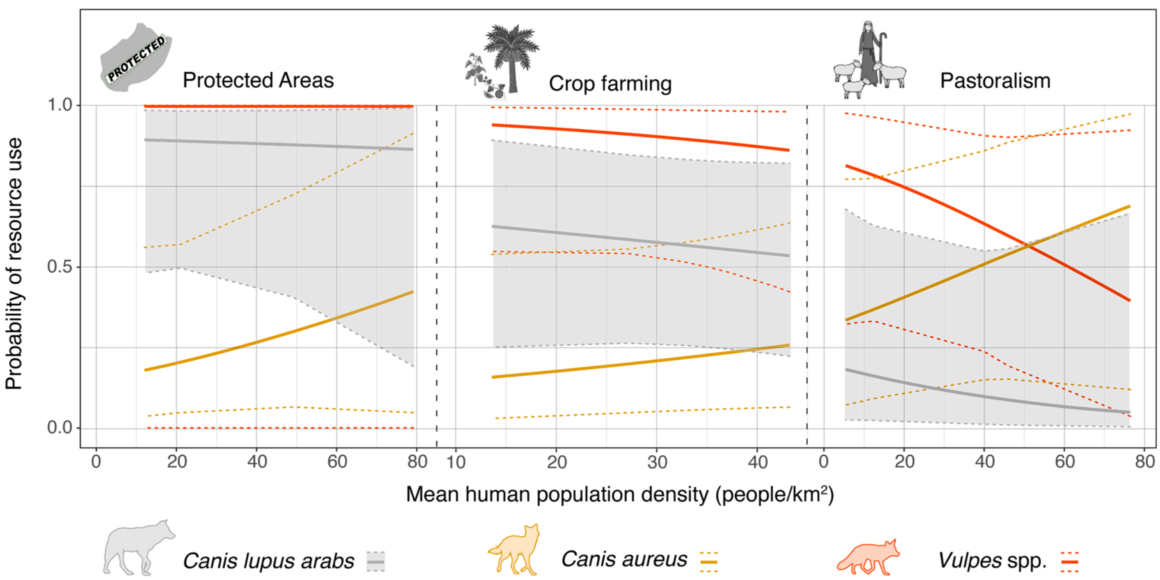


**Fig. 2.** Probabilities of resource use of canids across land-use categories as a function of human population density reveal that wolves (grey lines and shading) and foxes (red lines) are negatively influenced, while jackals (gold lines) are positively influenced, by human population density, particularly in pastoralist landscapes. Dashed lines represent 95 % confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

palm fronds attached, behind a slow-moving vehicle. We then converted the daily number of fresh tracks recorded per transect into the number of tracks/ha/day. Relative distribution (i.e., the proportion of area occupied) was estimated by scanning randomly selected 2-ha plots (31 in crop farming and 21 in pastoralist areas) and recording the presence or absence of tracks for each of the canid species.

## 3. Results

Based on a total of 418 canid events from 997 camera-trap days, we found that canid communities differed between human land uses (see Table A2). Most wolf (62.2%) and fox (54.4%) events were recorded in protected areas, whereas most jackal events were recorded in pastoralist landscapes (76.1%). Probability of resource use was similar for wolves and foxes: highest in protected areas, significantly higher in crop farming than pastoralist landscapes, and declining as human population density increased in agricultural

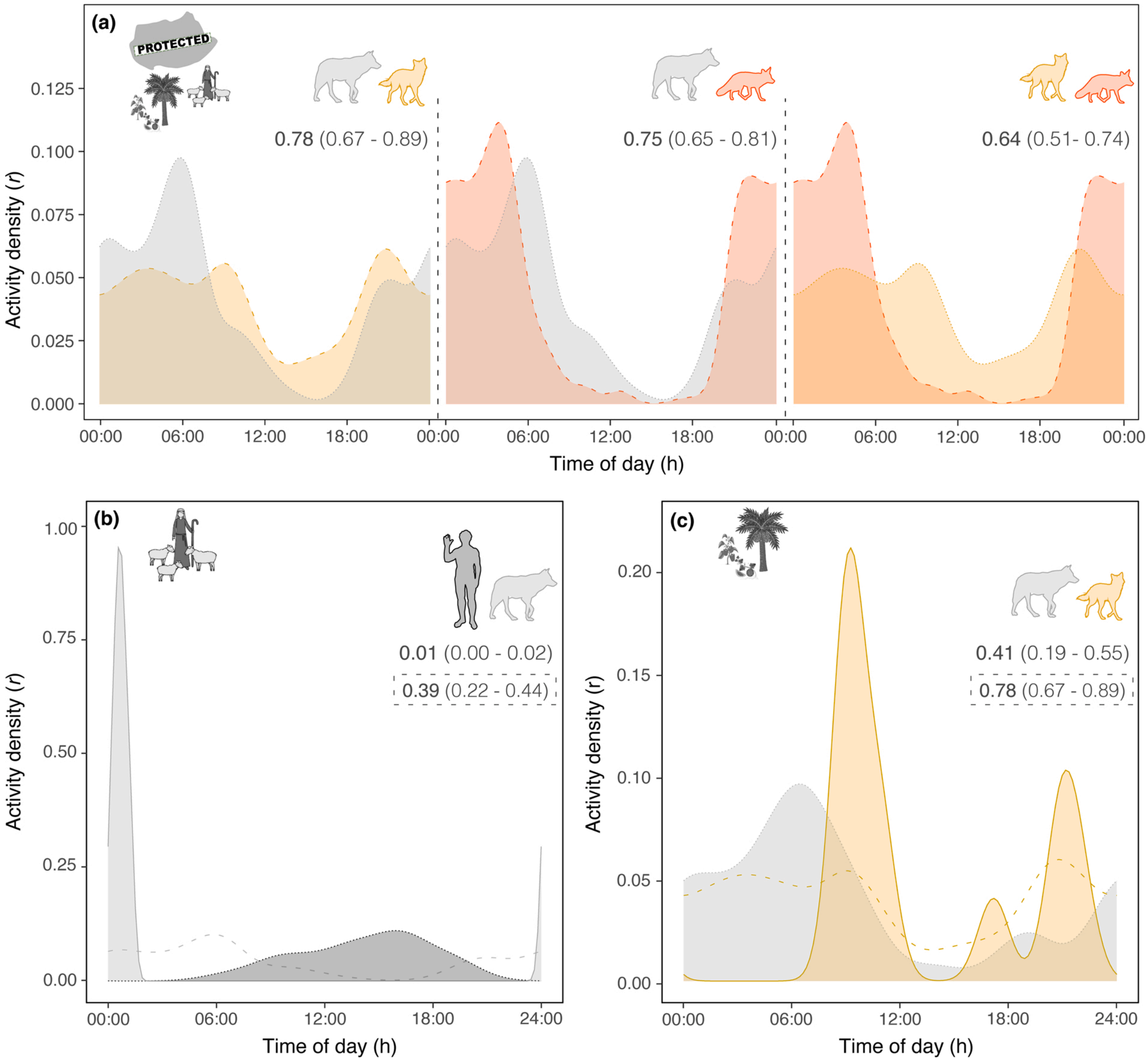


**Fig. 3.** Overlap in temporal activity patterns illustrating: (a) a relatively high temporal overlap between larger (dotted lines) and smaller (dashed lines) canids overall, where all canids are largely nocturnal with bimodal peaks in activity around dawn and dusk for wolves (grey lines and shading) and foxes (red lines and shading), and slightly later in the morning for jackals (gold lines and shading); (b) a significant shift in wolf (solid and dashed lines) activity in pastoralist landscapes to the middle of the night when people (dotted lines) were inactive; and (c) a significant shift in jackal (solid and dashed lines) activity in crop farming landscapes to times when wolves (dotted lines) were less active. Values denote bootstrapped coefficients of overlap ($\widehat{\Delta} \pm$ 95% CI), while dashed lines in (b) and (c) represent overall temporal activity patterns of smaller canid [dashed boxes represent overall coefficient of overlap ($\widehat{\Delta} \pm$ 95% CI)]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(crop farming and pastoralist) landscapes (Fig. 2). In contrast, the probability of resource use for jackals increased with human population density and was significantly higher in pastoralist landscapes than protected areas and crop farming landscapes (Fig. 2).

All canids were mostly nocturnal, with crepuscular peaks in activity (jackal activity was slightly later in the morning), and temporal overlap was generally high between canid pairs (Fig. 3a). However, wolf and jackal activity shifted significantly in pastoralist and crop farming landscapes, respectively (see Table A3). Temporal overlap between wolves and humans was low overall ($\widehat{\Delta} \pm 95\%$ CI = 0.39 ± 0.22 – 0.44) as humans were diurnal. However, overlap was particularly low in pastoralist landscapes where wolf activity shifted to a single peak in the middle of the night when humans were inactive ($\widehat{\Delta} \pm 95\%$ CI = 0.01 ± 0.00 – 0.02; Fig. 3b; Wald's $\chi^2 = 33.6$, $p < 0.0001$). Likewise, temporal overlap between wolves and jackals was lower in crop farming landscapes where jackal activity shifted to times of low wolf activity ($\widehat{\Delta} \pm 95\%$ CI = 0.41 ± 0.19 – 0.53; Fig. 3c; Wald's $\chi^2 = 16.5$, $p < 0.0001$).

Both jackals and foxes spatially avoided larger canids. At water points, fox avoidance of jackals was strongest (SIF = 0.34), followed by jackal avoidance of wolves (SIF = 0.72), and fox avoidance of wolves was the weakest (SIF = 0.82). Although the probability of resource use for foxes was highest at water points used by wolves, tracking surveys revealed that wolf and fox relative abundances were inversely related across agricultural landscapes in the Arava (Fig. 4). Wolves were more abundant in crop farming landscapes (Kruskal-Wallis $\chi^2 = 8.68$, $p < 0.01$; see Table A4), while foxes were more abundant in pastoralist landscapes (Kruskal-Wallis $\chi^2 = 11.40$, $p < 0.001$; see Table A4). Jackal abundance was equal, and lower than other canids, across both crop farming and pastoralist landscapes (Kruskal-Wallis $\chi^2 = 2.42$, $p = 0.12$; see Table A4).

## 4. Discussion

Our study demonstrates that Arabian wolves structure canid communities in the Middle East, and that this effect is intertwined with human land use and acceptance. We show that wolf persecution in pastoralist landscapes releases golden jackals from top-down pressure, which has cascading suppressive effects on foxes. Both wolves and jackals suppress foxes. We found that the relative abundance of foxes was lower where wolves were more abundant, and foxes avoided water points most used by jackals. Although Arabian wolves suppress foxes, they also indirectly facilitate foxes by lessening the suppressive force of jackals. These interactions, which are likely to have implications across multiple trophic levels, are contingent on human behaviour in these arid anthropogenic landscapes.

Wolves used protected areas most. Within agricultural areas, the probability of resource use and relative abundance of wolves were higher in crop farming than pastoralist landscapes. Similar to wolves, foxes used protected areas and crop farming landscapes most, and the probability of resource use of foxes declined with human population density in pastoralist landscapes. In contrast, the

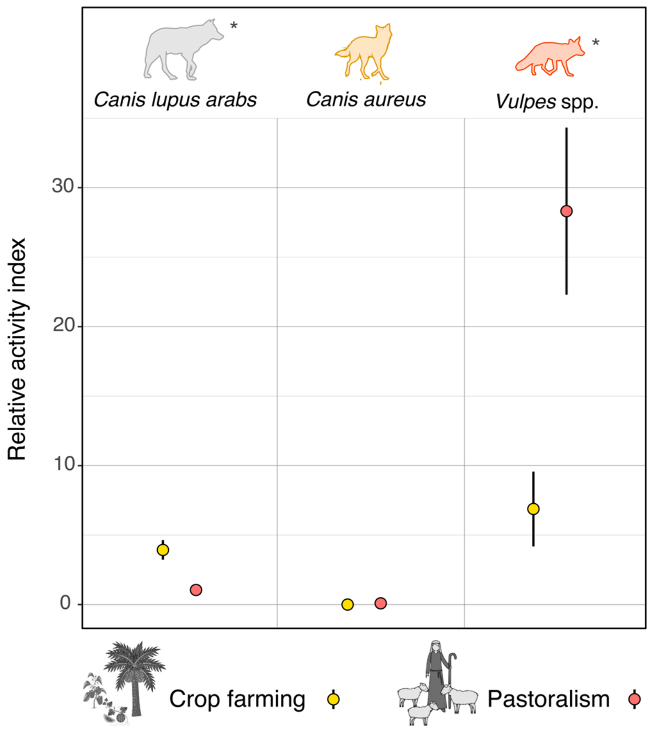


**Fig. 4.** Relative activity indices, calculated using the parameters estimated from tracking surveys, show that foxes in the Arava Valley are significantly more active in pastoralist landscapes than in crop farming landscapes where wolves are more active.

probability of resource use of jackals was lowest in protected areas and in crop farming landscapes, and the few jackal events that were recorded in crop farming landscapes coincided with times of low wolf activity. Unlike wolves and foxes, the probability of resource use of jackals increased with human population density. This aligns with the abundance of jackals around densely populated Israeli cities (Shamoon et al., 2017). Similarly, Shahnaseri et al. (2019) noted that in arid parts of Iran, the slightly larger Indian wolf (*C. l. pallipes*) avoided humans while jackals concentrated in agricultural areas.

We argue that jackals suppressed foxes in pastoralist landscapes with the highest human population densities in our study. Red foxes are consistently reported to have a strong affiliation with human activity, including previously from our study area (Shapira et al., 2008). In the USA, a regional study showed that coyotes and red foxes were both positively correlated along an urbanisation gradient (Rota et al., 2016); meanwhile, a fine-scale urban parklands study showed that red foxes benefit from using areas of high urban development as spatial refugia to reduce the chance of interference competition from coyotes (Moll et al., 2018).

Our study joins the internationally consistent observation that large canids suppress smaller canids. As European wolves suppress jackals (Krofel et al., 2017) and North American wolves suppress coyotes (Levi and Wilmers, 2012), Arabian wolves suppress jackals. The effects of wolf persecution cascade from wolves to jackals and to foxes in these desert canid communities. Our observation that wolves suppress jackals, releasing foxes from top-down control, parallels findings in North America where wolves mediate coyote suppression of foxes (Levi and Wilmers, 2012). Wolves were found to have a negligible effect on mesopredators in forested anthropogenic landscapes of Romania (Dorresteijn et al., 2015). However, the fact that jackals inhabit the region (Banea et al., 2012), but only foxes were recorded in the study, could provide further insights into interactions within the region's canid communities. We found that wolves influenced fox abundance in a region of the Arava Valley where jackals do not occur. Wolves were also noted to reduce fox abundance in parts of Sweden where jackals are absent, but only where wolf packs are stable and territories are well-established (Wikenros et al., 2017), as in the crop farming landscapes of the Arava Valley (Cohen et al., 2013).

In Europe, wolves avoid human-dominated landscapes (Carricondo-Sanchez et al., 2020; Dorresteijn et al., 2015). However, in crop farming landscapes of Israel's hyper-arid Arava Valley, Arabian wolves have previously been reported to spend most of their time in proximity to human infrastructure (Barocas et al., 2018), where they are subsidised by anthropogenic food and water resources (Lewin et al., 2021). We stress that the ability of wolves to do this is dependent on whether they are accepted by humans. In pastoralist landscapes, wolves are driven away from humans, and our results highlight the importance of protected areas among pastoralist landscapes (see also Bonsen and Khalilieh, 2021). We recorded few wolves in pastoralist landscapes, and those that occurred were around midnight, when humans were least active. Wildlife often become more nocturnal in anthropogenic landscapes to avoid human encounters (Gaynor et al., 2018). In our study, Arabian wolves increased their nocturnality where they were persecuted.

## 5. Conclusions

Our results indicate that, like their temperate cousins, Arabian wolves structure canid communities, and are therefore ecologically significant in arid environments. However, their ecological effects are most notable under conditions of human acceptance. Previous research focussing on relationships between humans and Arabian wolves has been limited, and comparisons had not been made between areas of varying acceptance. We show that, despite their relatively small size and the low productivity of the ecosystems they inhabit, Arabian wolves play key ecological roles where populations are stable. In contrast, the effects of such roles are considerably reduced in pastoralist landscapes where tolerance of wolves is low.

With things as they stand, Arabian wolf populations remain imperilled as pastoralism prevails as a predominant form of agriculture throughout its range. Jordan is an important jurisdiction for its conservation, as it provides a steppingstone between the stable population of the Arava Valley/Negev desert and the declining population of the Arabian Peninsula. The discovery of wolves successfully using protected areas in Jordan is potentially promising. Conservation efforts should focus on increasing tolerance and coexistence within pastoralist landscapes by promoting education around the ecological importance of the Arabian wolf and strategies towards coexistence. Reducing hunting rates, not only of wolves, but also their prey, is imperative as it would lead to the recovery of the wolf's natural prey base and alleviate the need for wolves to rely on livestock for sustenance. We hope that our research enhances protection of these animals in this unique part of the world so that Arabian wolves are not added to the list of predators recently lost from the Middle East.

## CRediT authorship contribution statement

**GTB, ADW, DR, DBA, OK, US,** and **AK** conceived and designed the study; **GTB, DBA, OK**, and **AK** collected field data; **GTB** and **DR** planned and performed the analyses with assistance from **ADW** and **EIFW**. **GTB** wrote the first draft of the manuscript and all authors provided valuable feedback and edits.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02139.

## References

Amr, Z.S., Hamidan, N., Quatrameez, M., 2004. Nature Conservation in Jordan. Biol. Linz/Austria 2, 467–477.

Banea, O.C., Krofel, M., Červinka, J., Gargarea, P., Szabó, L., 2012. New records, first estimates of densities and questions of applied ecology for jackals in Danube Delta Biosphere Reserve and hunting terrains from Romania. Acta Zool. Bulg. 64, 353–366.

Barocas, A., Hefner, R., Ucko, M., Merkle, J.A., Geffen, E., 2018. Behavioral adaptations of a large carnivore to human activity in an extremely arid landscape. Anim. Conserv. 1–11. https://doi.org/10.1111/acv.12414.

Berger, K.M., Gese, E.M., 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? J. Anim. Ecol. 76, 1075–1085. https://doi.org/10.1111/j.1365-2656.2007.01287.x.

Bonsen, G.T., Khalilieh, A., 2021. Towards improving conservation strategies for the endangered Arabian Wolf, Canis lupus arabs. Jordan J. Nat. Hist. 8, 47–50.

Boronyak, L., Jacobs, B., Wallach, A., 2020. Transitioning towards human–large carnivore coexistence in extensive grazing systems. Ambio. https://doi.org/10.1007/s13280-020-01340-w.

Carricondo-Sanchez, D., Zimmermann, B., Wabakken, P., Eriksen, A., Milleret, C., Ordiz, A., Sanz-Perez, A., Wikenros, C., 2020. Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features. Biol. Conserv. 244, 108514 https://doi.org/10.1016/j.biocon.2020.108514.

Chapron, G., Kaczensky, P., Linnell, J.D.C., Arx, M., von, Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balciauskas, L., Balys, V., Bedo, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremic, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majic, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Myslajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunovic, M., Persson, J., Potocnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinsek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Vána, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346 (80), 1517–1519. https://doi.org/10.1016/S0169-5347(01)02290-X.

Cohen, O., Barocas, A., Geffen, E., 2013. Conflicting management policies for the Arabian wolf Canis lupus arabs in the Negev Desert: is this justified? Oryx 47, 228–236. https://doi.org/10.1017/S0030605311001797.

Colman, N.J., Gordon, C.E., Crowther, M.S., Letnic, M., 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. Proc. R. Soc. B Biol. Sci. 281. https://doi.org/10.1098/rspb.2013.3094.

Cunningham, P., Wronski, T., Al Aqeel, K., 2009. Predators persecuted in the Asir Region, South-western Saudi Arabia. Wildl. Middle East News 4, 6.

Dorresteijn, I., Schultner, J., Nimmo, D.G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L., Ritchie, E.G., 2015. Incorporating anthropogenic effects into trophic ecology: predator-prey interactions in a human-dominated landscape. Proc. R. Soc. B 282, 20151602. https://doi.org/10.1098/rspb.2015.1602.

Eid, E., Handal, R., 2018. Illegal hunting in Jordan: Using social media to assess impacts on wildlife. Oryx 52, 730–735. https://doi.org/10.1017/S0030605316001629.

ESRI, 2019. ArcGIS Desktop: Release 10.8. Environmental Systems Research Institute, Redlands, CA, USA.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Hojnowski, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science 360, 1232–1235. https://doi.org/10.1126/science.aar7121.

Gecchele, L.V., Bremner-Harrison, S., Gilbert, F., Soultan, A., Davison, A., Durrant, K.L., 2017. A pilot study to survey the carnivore community in the hyper-arid environment of South Sinai mountains. J. Arid Environ. 141, 16–24. https://doi.org/10.1016/j.jaridenv.2017.01.009.

George, K.A., Slagle, K.M., Wilson, R.S., Moeller, S.J., Bruskotter, J.T., 2016. Changes in attitudes toward animals in the United States from 1978 to 2014. Biol. Conserv. 201, 237–242. https://doi.org/10.1016/j.biocon.2016.07.013.

Heath, M.R., Speirs, D.C., Steele, J.H., 2014. Understanding patterns and processes in models of trophic cascades. Ecol. Lett. 17, 101–114. https://doi.org/10.1111/ele.12200.

Hefner, R., Geffen, E., 1999. Group size and mome range of the Arabian wolf (Canis lupus) in southern Israel. J. Mammal. 80, 611–619.

Krofel, M., Giannatos, G., Cirovic, D., Stoyanov, S., Newsome, T.M., 2017. Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution? Hystrix Ital. J. Mammal. 28, 9–15. https://doi.org/10.4404/hystrix.

Levi, T., Wilmers, C.C., 2012. Wolves-coyotes-foxes: a cascade among carnivores Wolves – coyotes – foxes: a cascade among carnivores. Ecology 93, 921–929. https://doi.org/10.2307/23213740.

Lewin, A., Erinjery, J.J., le Polain de Waroux, Y., Tripler, E., Iwamura, T., 2021. Land-use differences modify predator-prey interactions and Acacia vegetation in a hyperarid ecosystem. J. Arid Environ. 192 https://doi.org/10.1016/j.jaridenv.2021.104547.

Mackenzie, D.I., 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. J. Wildl. Manag. 70, 367–374. https://doi.org/10.2193/0022-541x(2006)70[367:mtporu]2.0.co;2.

Magory Cohen, T., King, R., Dolev, A., Boldo, A., Lichter-Peled, A., Kahila Bar-Gal, G., 2013. Genetic characterization of populations of the golden jackal and the red fox in Israel. Conserv. Genet. 14, 55–63. https://doi.org/10.1007/s10592-012-0423-1.

Mallon, D., Budd, K., 2011. Regional Red List Status of Carnivores in the Arabian Peninsula, 1–52.
Meredith, M., Ridout, M.S., 2020. Overview of the overlap package. R. Proj. 1–9.
Moll, R.J., Cepek, J.D., Lorch, P.D., Dennis, P.M., Robison, T., Millspaugh, J.J., Montgomery, R.A., 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosyst. 1–14. https://doi.org/10.1007/s11252-018-0758-6.
Nemtzov, S.C., King, R., 2001. Management of wild canids (fox, jackal and wolf) in Israel, with respect to their damage to agriculture, and to the spread of rabies. Adv. Vertebr. Pest Manag. ii, 219–230 https://doi.org/papers://A270C103-A120-4E61-B0FE-19A2B90778C5/Paper/p3623.
Newsome, T.M., Greenville, A.C., Ćirović, D., Dickman, C.R., Johnson, C.N., Krofel, M., Letnic, M., Ripple, W.J., Ritchie, E.G., Stoyanov, S., Wirsing, A.J., 2017. Top predators constrain mesopredator distributions. Nat. Commun. 8, 1–7. https://doi.org/10.1038/ncomms15469.
Newsome, T.M., Ripple, W.J., 2015. A continental scale trophic cascade from wolves through coyotes to foxes. J. Anim. Ecol. 84, 49–59. https://doi.org/10.1111/1365-2656.12258.
R Core Team, 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Richmond, O.M.W., Hines, J.E., Beissinger, S.R., 2010. Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. Ecol. Appl. 20, 2036–2046. https://doi.org/10.1890/09-0470.1.
Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14, 322–337. https://doi.org/10.1198/jabes.2009.08038.
Ripple, W.J., Beschta, R.L., 2011. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biol. Conserv. 145. https://doi.org/10.1016/j.biocon.2011.11.005.
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 (80), 1241484. https://doi.org/10.1126/science.1241484.
Rota, C.T., Ferreira, M.A.R., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W., Millspaugh, J.J., 2016. A multispecies occupancy model for two or more interacting species. Methods Ecol. Evol. 7, 1164–1173. https://doi.org/10.1111/2041-210X.12587.
Sakurai, R., Tsunoda, H., Enari, H., Siemer, W.F., Uehara, T., Stedman, R.C., 2020. Factors affecting attitudes toward reintroduction of wolves in Japan. Glob. Ecol. Conserv. 22. https://doi.org/10.1016/j.gecco.2020.e01036.
Scheinin, S., Yom-Tov, Y., Motro, U., Geffen, E., 2006. Behavioural responses of red foxes to an increase in the presence of golden jackals: a field experiment. Anim. Behav. 71, 577–584. https://doi.org/10.1016/j.anbehav.2005.05.022.
Shahnaseri, G., Hemami, M.R., Khosravi, R., Malakoutikhah, S., Omidi, M., Cushman, S.A., 2019. Contrasting use of habitat, landscape elements, and corridors by grey wolf and golden jackal in central Iran. Landsc. Ecol. 34, 1263–1277. https://doi.org/10.1007/s10980-019-00831-w.
Shamoon, H., Saltz, D., Dayan, T., 2017. Fine-scale temporal and spatial population fluctuations of medium sized carnivores in a Mediterranean agricultural matrix. Landsc. Ecol. 32, 1–14. https://doi.org/10.1007/s10980-017-0517-8.
Shapira, I., Sultan, H., Shanas, U., 2008. Agricultural farming alters predator-prey interactions in nearby natural habitats. Anim. Conserv. 11, 1–8. https://doi.org/10.1111/j.1469-1795.2007.00145.x.
Wallach, A.D., Johnson, C.N., Ritchie, E.G., O'Neill, A.J., 2010. Predator control promotes invasive dominated ecological states. Ecol. Lett. 13, 1008–1018. https://doi.org/10.1111/j.1461-0248.2010.01492.x.
Wallach, A.D., Ritchie, E.G., Read, J., O'Neill, A.J., 2009. More than mere numbers: the impact of lethal control on the social stability of a top-order predator. PLoS One 4. https://doi.org/10.1371/journal.pone.0006861.
Wikenros, C., Aronsson, M., Liberg, O., Jarnemo, A., Hansson, J., Wallgren, M., Sand, H., Bergström, R., 2017. Fear or food - abundance of red fox in relation to occurrence of lynx and Wolf. Sci. Rep. 7, 1–10. https://doi.org/10.1038/s41598-017-08927-6.
Wooster, E.I.F., Ramp, D., Lundgren, E.J., O'Neill, A.J., Wallach, A.D., 2021. Red foxes avoid apex predation without increasing fear. Behav. Ecol. https://doi.org/10.1093/beheco/arab053.