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Predator foraging response to a resurgent dangerous prey

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Summary

1. Prey switching occurs when a generalist predator kills disproportionately more of an abundant prey species and correspondingly spares a rarer species. Although this behaviour is a classic stabilizing mechanism in food web models, little is known about its operation in free-living systems which often include dangerous prey species that resist predation.

2. We used long-term (1995–2015) data from a large mammal system in northern Yellowstone National Park, USA, to understand how prey preference of a wild, generalist predator (*Canis lupus*) responds to a shift in prey species evenness involving rising numbers of dangerous prey (*Bison bison*) and dropping numbers of relatively safer prey (*Cervus elaphus*).

3. Contrary to the prey switching hypothesis, wolves attacked and killed disproportionately more of the rarer, but safer, species. Wolves maintained a strong preference against bison even when this species was nearly twice as abundant as elk. [Correction added after online publication on 26 April 2017: 'more than' changed to 'nearly']. There was also evidence that wolves were increasingly averse to hunting bison as relative bison abundance increased.

4. Wolves seldom hunted bison because capture success was limited to a narrow set of conditions: larger packs (>11 wolves) chasing smaller herds (10–20 bison) with calves. Wolves scavenged bison carrion instead and did so more frequently as bison abundance increased.

5. Our study demonstrates the overarching importance of prey vulnerability to understanding the prey preferences of generalist predators in ecological communities with dangerous prey. The formidable defences of such prey diminish the potential for switching and its stabilizing influence on population dynamics. In these communities, shifts from hunting to scavenging are perhaps more likely than shifts in prey preference. The assumption of switching may therefore overestimate the stability of multi-prey systems that include dangerous prey species.

Key-words: antipredator behaviour, bison, dangerous prey, elk, frequency-dependent predation, prey switching, prey vulnerability, scavenging, wolves, Yellowstone National Park

Introduction

A classic hypothesis in ecology is that generalist predators stabilize prey populations by 'switching' between prey as the prey species' relative abundances change (Murdoch 1969; Murdoch & Oaten 1975). Switching occurs when preference for a prey species (defined as the relative frequency of finding, attacking and capturing prey) becomes stronger or weaker as that species forms a larger or smaller proportion of available prey (Murdoch 1969; Murdoch & Oaten 1975). This means the predator directs a disproportionate number of its attacks to the more abundant species and correspondingly spares the rarer species. Although switching is often invoked to stabilize population dynamics in food web models (e.g. Valdovinos *et al.* 2010; van Leeuwen *et al.* 2013; Morozov & Petrovskii 2013), empirical evidence of switching is not well-developed. Much of it is based on experimental studies of small taxa that are helpless when attacked by a predator (reviewed by Garrott *et al.* 2007). This is problematic because many free-living systems include dangerous prey species that can harm or kill their predators (Mukherjee & Heithaus 2013) and interspecific differences in prey

*Correspondence author. E-mail: aimeetmt@gmail.com vulnerability may have an overriding influence on predator preference that prevents switching (Becker *et al.* 2009).

Many prey species are dangerous, and accumulating evidence suggests that predators often select prey that minimize the risk of injury, rather than maximize intake rate (Rutten *et al.* 2006; Mukherjee & Heithaus 2013). The potentially high fitness costs associated with attacking dangerous prey, including the extra time necessary to safely handle them, may cause preference for them to lag behind increases in their relative abundance. As a result, predators may concentrate a disproportionate number of attacks on the rarer but safer prey. The extent that preference decouples from relative abundance ultimately depends on the ability of predators to overcome prey antipredator defences. If these defences are robust, predator preference may increase slowly, or even decrease, if predators shift from hunting dangerous prey to scavenging them as carrion (Pereira, Owen-Smith & Moleón 2014). This is a broadly important issue in ecology and conservation because climate change, variable culling rates, species invasions, (re)introductions and recoveries can all modify the species composition and evenness of prey communities in ways that allow dangerous prey to predominate (e.g. Crossland 2000; Ripple *et al.* 2010; Albins & Hixon 2013).

In northern Yellowstone National Park, for example, multi-year drought, culling outside the park, wolf (*Canis lupus*) reintroduction and natural recovery of grizzly bears (*Ursus arctos*) and cougars (*Puma concolor*) have decreased the abundance of elk (*Cervus elaphus*) (MacNulty *et al.* 2016), whereas immigration/redistribution, high survival and recruitment and low predation rates have increased the abundance of bison (*Bison bison*) (Geremia, Wallen & White 2015; White, Wallen & Hallac 2015). Predictions about the impact of wolf reintroduction on elk abundance in northern Yellowstone hinge on the untested assumption that wolves switch between elk and bison (Garton *et al.* 1990; Boyce 1993, 1995; Messier 1995; Varley & Boyce 2006). However, bison are the largest, most dangerous native ungulate species in North America (Mech, Smith & MacNulty 2015). A high and constant proportion (96% during winter) of elk among prey killed by wolves in northern Yellowstone from 1995 to 2009, together with a tendency for wolves to scavenge bison carrion (Metz *et al.* 2012), suggests this assumption is unfounded. On the other hand, bison abundance did not rival elk abundance until after 2009 (Geremia, Wallen & White 2015; Northern Yellowstone Cooperative Wildlife Working Group 2016).

Here, we used long-term data (1995–2015) on wolf hunting behaviour, wolf-killed prey and elk and bison abundances to test for prey switching behaviour in a dangerous prey system. We measured how wolf preference responded to increasing numbers of bison in northern Yellowstone by relating the relative abundance of bison and elk to the ratios of the two species attacked and killed by wolves. We calculated attack ratios from observations of wolf hunting behaviour and kill ratios from carcasses attributed to wolf predation. To understand underlying controls on wolf preference for bison, we also examined how (i) the behavioural and life-history traits of bison (flight response, herd size, age and sex) and wolves (pack size) shaped the ability of wolves to attack and capture them, and (ii) bison abundance affected wolf scavenging behaviour.

Materials and methods

STUDY AREA

Our study focused on the wolves, elk and bison that inhabit the winter range of northern Yellowstone. This 1520-km^2 area is defined by the low-elevation (1500–2600 m) grasslands and shrub steppes that fan out from the Yellowstone River and its tributaries along the northern border of Yellowstone National Park and adjacent areas in Montana (Lemke, Mack & Houston 1998). Approximately 65% (995 km^2) of the winter range is located within the park, whereas the remaining 35% (525 km^2) extends north of the park boundary. For the purposes of this study, we refer to the entire northern Yellowstone elk winter range as the ‘total winter range’ and the park portion of this area as the ‘park winter range’ (Fig. 1).

Northern Yellowstone elk migrate seasonally, moving from higher-elevation summer ranges to lower-elevation areas throughout the total winter range (White *et al.* 2010). Northern Yellowstone bison similarly seek lower-elevation areas in winter, except their distribution is mainly restricted to the park winter range by management intervention in response to concerns of brucellosis transmission to cattle outside the park (White, Wallen & Hallac 2015). Wolves were reintroduced to Yellowstone in 1995–1997 (Bangs & Fritts 1996) and their distribution is also concentrated in the park winter range (Stahler, Smith & Stahler 2016). Wolf abundance in northern Yellowstone ranged between 19 and 98 individuals (Smith *et al.* 2016). Besides elk and bison, wolves occasionally killed deer (*Odocoileus* spp.), bighorn sheep (*Ovis canadensis*), moose (*Alces alces*) and pronghorn (*Antilocapra americana*) (Metz *et al.* 2012). All wolf predation data in our prey switching analysis were collected in the park winter range. Elk abundance data were collected across the total winter range and the location of elk sightings was used to determine elk abundance in the park winter range (see below).

Because wolves were rarely observed hunting bison in northern Yellowstone (Smith *et al.* 2000), our analysis of wolf-bison behavioural interactions includes data collected in Pelican Valley. This 100-km² area is located in the central portion of the park at 2500 m, north of Yellowstone Lake (Fig. 1). We often observed wolves hunting bison in Pelican Valley during winter because alternate prey were scarce (MacNulty *et al.* 2014).

DATA COLLECTION

Prey abundance

Bison were counted during annual aerial winter surveys, conducted by one or two fixed-wing aircraft between 19 January and 10 March, 1995–2015 (Geremia *et al.* 2014). Uncorrected count data provided an unbiased measure of bison abundance because bison formed large groups that congregated in visible, open areas (Hess 2002). If any bison were culled at the northern park boundary during winter prior to a flight, we added the number culled to the aerial count (Geremia, Wallen & White 2015).

Elk were counted during annual aerial winter surveys, conducted by 3–4 fixed-wing aircraft, each simultaneously flying non-overlapping areas between 3 December and 7 March, 1995–2015 (see Northern Yellowstone Cooperative Wildlife Working Group

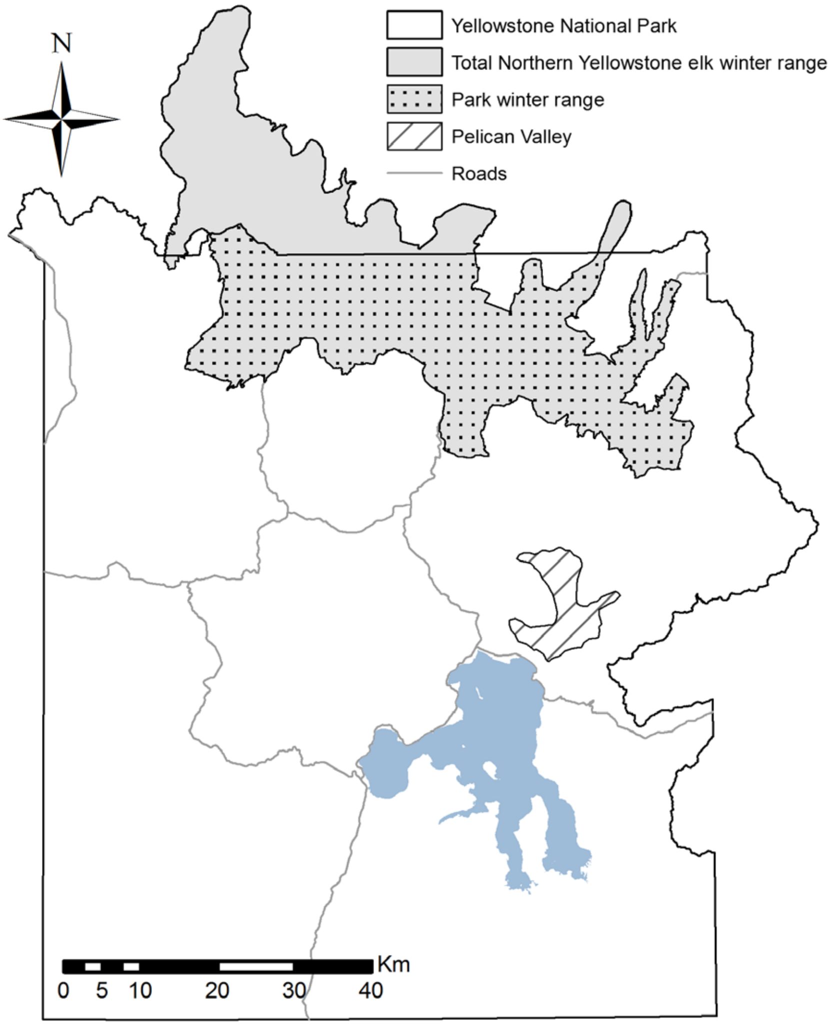

Fig. 1. Yellowstone National Park including the northern Yellowstone elk winter range and Pelican Valley areas that were the focus of this study.

2016). We used a state–space model to interpolate elk counts for years when no survey occurred (1996, 1997, 2006, 2014), then applied a modified version of the Singer & Garton (1994) northern Yellowstone elk sightability model to adjust every count for imperfect detection (see Supporting Information Appendix S1 for details). 'Total' and 'park' elk abundances refer to the estimated number of elk within the total and park winter ranges, respectively (see Table S1). We separately measured the relative abundance of bison and elk ($N_{\mathrm{bison}}/N_{\mathrm{elk}}$) in the total and park winter ranges to account for variation in numbers of elk migrating outside the park. This approximated the minimum and maximum ratios of their abundances in the park winter range where we measured wolf prey preference.

Prey preference

We measured annual variation in the ratios of elk and bison attacked and killed by wolves in the park winter range between 1995 and 2015 with data collected (i) during biannual 30-day follows of three to five wolf packs from the ground and fixed-wing aircraft in early (mid-November to mid-December) and late (March) winter, and (ii) during opportunistic ground and aerial surveys of all wolf packs throughout the entire winter (Smith *et al.* 2004). We defined winter as 1 November–30 April. Field crews used radiotelemetry to monitor packs. At least one wolf in each pack was fitted with a VHF (very high-frequency) radiocollar. Wolves were captured and handled following animal handling guidelines of the American Society of Mammalogists (Sikes, Gannon & Amer Soc 2011) and approved by the National Park Service Institutional Animal Care and Use Committee (Permit: IMR_Yell_Smith_Wolf_2012). Over the 20-year study, 30 different packs inhabited northern Yellowstone; 18 were intensively monitored.

Field crews identified elk and bison carcasses and recorded cause of death, date of death, species, sex and age. Cause of death was 'wolf-killed' when wolves were observed making the kill, or evidence at the carcass site supported wolves as the cause of death. This included chase tracks, blood trails, disturbed vegetation and extensive disarticulation of the carcass. Cougar kills were generally discernable by evidence that cougars had cached a carcass. Grizzly bears and black bears also occasionally kill ungulates, but usually not in winter when bears are denning. We excluded scavenged carcasses from analyses of prey switching because switching concerns changes in predatory behaviour. Field crews documented 2687 carcasses of elk and 52 carcasses of bison killed by wolves. We used these data to calculate the annual ratio of bison and elk killed by wolves ($g_{\mathrm{bison}}/g_{\mathrm{elk}}$; 'relative kill frequency').

Carcasses of non-wolf killed ungulates with obvious amounts of consumable biomass were identified as 'wolf-scavenged' if they were visited by wolves. Carcass biomass was determined by visual observation, duration of wolf visit and the presence and abundance of other scavenger species (e.g. *Corvus corax*, *Canis latrans*). Between 1995 and 2015, field crews documented 137 bison carcasses scavenged by wolves.

When field crews observed wolves encountering elk (or bison), defined as at least one wolf orienting and moving (walking, trotting or running) towards prey, they followed the progress of the encounter by noting the foraging state (approach, watch, attack-group, attack-individual or capture) of the individual(s) closest to making a kill (see MacNulty, Mech & Smith 2007). We scored an encounter as escalating to an attack if more than one wolf transitioned from approach (or watch) to attack-group (or attack-individual) at any time during the encounter. This yielded 964 attacks of elk and 178 attacks of bison. We used these data to calculate the annual ratio of bison and elk attacks ($a_{\text{bison}}/a_{\text{elk}}$; 'relative attack frequency'). Within the park winter range, wolf encounter rate with elk covaried with elk abundance (Martin 2016).

Wolf–bison behavioural interactions

A subset of wolf–bison encounters included detailed information about the sequential occurrence of each foraging state during each encounter, and the traits of wolves (group size) and bison (group size, age, sex and behavioural response) involved in those states. We used these data to understand how these traits governed the ability of wolves to attack and capture bison. In this case, the unit of analysis was the foraging state, and we examined how traits influenced the probability of a state transition that corresponded to 'attacking' (approach [or watch] → attack-group [or attack-individual]) or 'capturing' (attack-group [or attack-individual] → capture). Capturing was not necessarily killing because bison that were grabbed by wolves often escaped (see MacNulty, Mech & Smith 2007).

A wolf was scored as participating in a foraging state if it exhibited the behavioural acts characterizing that particular state as described by MacNulty *et al.* (2014: table 1; Fig. 1). We considered non-participation in a given state as when a wolf was in view but engaged in another foraging state or a non-predatory behaviour (e.g. resting). We defined 'wolf group size' as the number of wolves participating in a foraging state. This differs from pack size because it pertains to the subset of pack members participating in a hunt.

We defined 'bison group size' as the number of bison within 100 m of one another (Fortin *et al.* 2003) that were present at the end of each foraging state. We used body size and horn morphology to identify three age/sex classes: bull, cow and calf. In winter, bulls aggregate in small bull-only groups separate from larger mixed age–sex groups of cows, immature bulls and calves (Meagher 1973). Accordingly, we defined the age–sex composition of each bison group in each foraging state as 'bull' or 'mixed'.

We recorded two types of bison behavioural responses during each foraging state. The 'charge response' considered whether or not more than one adult member of a bison group charged (ran) at wolves. The 'flight response' considered whether a group fled or stood and confronted wolves. We scored a group as fleeing if >50% of the group ran or walked away from wolves.

Our detailed wolf–bison encounter data are based on observations of five different wolf packs (Druid Peak, Geode Creek, Leopold, Mollie's, and Rose Creek) hunting in northern Yellowstone (1996–2003) and Pelican Valley (1999–2013). Most of these observations (75% of 187 wolf–bison encounters) involved the Mollie's pack in Pelican Valley. Annual turnover in pack membership due to births, deaths and dispersal minimized the influence of pack identity on the outcome of wolf–bison encounters.

DATA ANALYSIS

Prey switching

We conducted two separate tests for prey switching behaviour, which is defined by an increase in a predator's preference for a prey species that is disproportionate to the increase in the relative abundance of that prey species (Murdoch 1969; Murdoch & Oaten 1975). Our first test examined the relationship between relative attack frequency ($a_{\text{bison}}/a_{\text{elk}}$) and relative bison abundance ($N_{\text{bison}}/N_{\text{elk}}$). If switching occurred, relative attack frequency should increase as a curvilinear function of relative bison abundance. We tested this prediction by comparing a simple linear model of this relationship with a linear model with log-transformed relative bison abundance using Akaike's Information Criterion, AIC_c (Burnham & Anderson 2002).

Our second test examined the relationship between relative kill frequency ($g_{\text{bison}}/g_{\text{elk}}$) and relative bison abundance using Murdoch's (1969) classic diet equation as modified by Greenwood & Elton (1979) and Elliott (2004):

$$\frac{g_{\text{bison}}}{g_{\text{elk}}} = \left(c\frac{N_{\text{bison}}}{N_{\text{elk}}}\right)^{b}$$

where $g_{\text{bison}}/g_{\text{elk}}$ is the ratio of bison and elk killed by wolves, and $N_{\text{bison}}/N_{\text{elk}}$ is the ratio of bison and elk in the environment. The variable c measures the bias in wolf kills towards one species: $c > 1$ indicates preference for bison, whereas $c < 1$ indicates preference for elk. The variable b measures the extent of switching such that $b > 1$ indicates a switch to bison as relative bison abundance increases. This is visualized as a curvilinear, concave-up relationship between relative kill frequency and relative bison abundance. We fit the diet equation to our data and estimated parameter coefficients using nonlinear least squares regression.

We performed each test separately for the relative abundance of bison across the total and park winter ranges. Data were annual estimates of relative attack and kill frequencies, and relative bison abundance ($N = 20$ years).

Wolf–bison behavioural interactions

We analysed the effects of wolf and bison traits on the probability that wolves attacked and captured bison using generalized linear mixed models (GLMMs) with a binomial error distribution. We constructed these models to account for the influence of unmeasured pack- and encounter-related factors on hunting success (e.g. age and size of individuals within packs; MacNulty *et al.* 2009a, b) and differences in prey densities between pack territories. All models fitted pack and encounter identity as nested random intercepts (encounter within pack) and included a compound symmetric correlation structure which assumed that all observations within encounters were, on average, equally correlated (Weiss 2005). Capture models included only a random intercept for encounter identity because our sample was too small to support a multivariate GLMM with more than one random effect. We estimated models with adaptive Gaussian quadrature with parameters estimated from maximum likelihood, and significance of effects determined by an approximate z-test.

Models of attacking and capturing included fixed effects for three bison traits (group size and composition, flight response) and one wolf trait (group size). To account for the possibility that carnivore hunting success peaks at intermediate ungulate group sizes (Creel & Creel 2002; Hebblewhite & Pletscher 2002), we used restricted cubic splines ($N_{\text{knots}} = 3$) to test for a nonlinear effect of bison group size on the probabilities of attack and capture. We tested the strength of these effects with likelihood ratio statistics.

We modelled bison group composition (bull vs. mixed) and flight response (flee vs. confront) as dummy variables. We expected the probabilities of attack and capture to be greatest for mixed groups and for bison that fled because mixed groups include vulnerable calves (Carbyn & Trottier 1987; Becker *et al.* 2009) and wolves are often intimidated by ungulates that stand and fight (Mech, Smith & MacNulty 2015). We modelled the effect of wolf group size as a piecewise linear spline with knots at 4 and 11 for attacking and capturing following MacNulty *et al.* (2014).

To evaluate the relative influence of wolf and bison traits in our models of attack and capture, we performed a sensitivity analysis that allowed comparison of effects across a common scale. First, we calculated the predicted probability of attack (or capture) with wolf and bison group sizes set to observed means and categorical variables, bison group composition and flight response, set to ‘mixed’ and ‘flee’. Next, we separately perturbed each model parameter by 10%, recalculated the prediction and computed the difference between the initial and perturbed prediction. A large difference indicates a high sensitivity, and parameters with the highest sensitivity had the greatest effect on the ability of wolves to attack (or capture). We report absolute sensitivity values and sum those for spline parameters to show the overall influence of a nonlinear effect and to allow comparison between linear and nonlinear effects (Stahler *et al.* 2013).

We also used GLMMs to evaluate potential differences in the behavioural responses of bull and mixed groups when attacked by wolves. Anecdotal evidence suggests that bulls are generally more aggressive towards wolves than cows (Carbyn, Oosenbrug & Anions 1993). We expected bull groups to charge more and flee less in response to wolf attack relative to mixed groups. Models included covariates for bison and wolf group sizes to control for their potential effects on bison response.

Wolf–bison scavenging

To determine the effects of scavenging on prey switching behaviour, we examined how annual bison attack and kill frequencies varied with the number of wolf-scavenged bison. We compared linear and nonlinear (log-transformed scavenged bison) models of this relationship using $\mathrm{AIC_c}$.

Results

TEMPORAL TRENDS

Prey abundance

Numbers of bison in the northern Yellowstone park winter range increased from 681 in 1995–1996 to 2164 in 2014–2015 (Fig. 2a). During this same period, sightability-corrected elk numbers decreased from 15 913 to 1853 in the park winter range. Numbers of elk wintering outside the park varied between 2449 and 5147 (mean ± SE = 3539 ± 163 elk) and exhibited no overall trend. There was an upward trend after 2011 and this contributed to a shift in winter distribution, with most elk (61–73%)

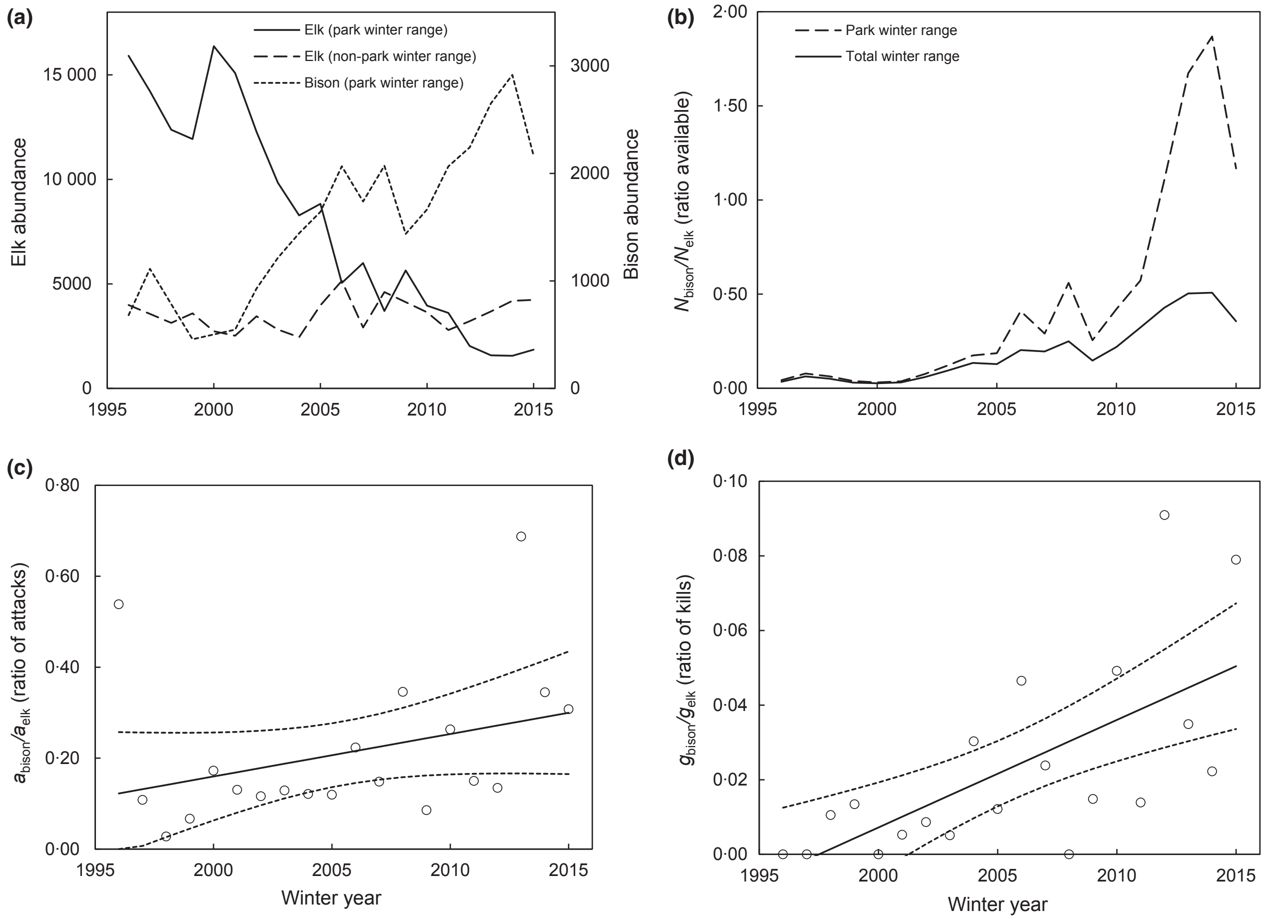

Fig. 2. Trends in bison and elk abundance in the park and non-park portions of the northern Yellowstone elk winter range (a), relative bison and elk abundance in the total and park winter ranges (b), relative frequency of wolf attacks on bison and elk in the park winter range (c) and relative frequency of bison and elk killed by wolves in the park winter range (d) during winter (1 November–30 April), 1995–2015. ‘Winter year’ starts 1 January (e.g. 1996 represents the 1 November–30 April, 1995–1996 winter year). In (c) and (d), open circles are observed values and solid lines are fitted values with dotted lines indicating 95% confidence intervals.

located outside the park during 2012–2015 (Fig. 2a). Thus, the overall decline in elk abundance across the total winter range ($N_{1995–1996}$ = 19 904 elk; $N_{2014–2015}$ = 6090 elk) mainly reflects decreased elk abundance within the park winter range (Fig. 2a). This explains why the increase in relative bison abundance was greater in the park winter range than in the total winter range (Fig. 2b). Relative bison abundance in the park winter range increased from 0·04 bison per elk in winter 1995–1996 to 1·17 bison per elk in winter 2014–2015. By contrast, relative bison abundance in the total winter range increased from 0·03 bison per elk in winter 1995–1996 to 0·36 bison per elk in winter 2014–2015.

Attack frequency

Direct observations of wolf–prey encounters in the park winter range indicated that the overall frequency of wolves attacking bison (41% of 436 bison encounters) was less than that of wolves attacking elk (67% of 1434 elk encounters). Nevertheless, the relative frequency that wolves attacked bison vs. elk tended to increase over the study (r^2 = 0·11; range = 0·03–0·69; Fig. 2c). Relative attack frequency was notably high in 1995–1996 (0·54) and 2012–2013 (0·69). Excluding these outliers strengthened the upward trend in relative attack frequency (r^2 = 0·45). Annual number of attacks ranged between 1 and 37 (8·2 ± 1·8 attacks/year) for bison, and 13 and 107 (48·2 ± 6·5 attacks/year) for elk.

Kill frequency

Although bison comprised only 2% of 2739 carcasses of elk and bison killed by wolves, the relative frequency of bison kills tended to increase from 1995–1996 to 2014–2015 (r^2 = 0·37; range = 0·00–0·11; Fig. 2d). Annual number of kills ranged from 0 to 10 (2·6 ± 0·59 kills/year) for bison, and 76 to 236 (134·4 ± 9·8 kills/year) for elk. The 52 bison kills included 7 calves, 28 cows, 7 bulls and 10 adults of unknown sex. Mean (±SE) age (years) of known individuals for each age/sex class was 7·95 ± 1·00 for cows (N = 20), 8·83 ± 2·30 for bulls (N = 6) and 5·00 ± 0·58 for unknown adults (N = 3).

PREY SWITCHING

Despite the suggestive temporal trends in relative attack and kill frequencies (Fig. 2c,d), we found no quantitative evidence of prey switching. The most parsimonious models of relative attack frequency in the total and park winter ranges included a linear effect of relative bison abundance, indicating that the relative frequency that wolves attacked bison increased proportionately to relative bison abundance (Fig. 3a,b). Evidence against a model describing a nonlinear relationship between relative attack frequency and relative bison abundance was reasonably strong in the total ($\Delta AIC_c = 3·23$) and park ($\Delta AIC_c = 4·29$) winter ranges. Excluding the outlying data points from 1995–1996 and 2012–2013 improved the fit of these nonlinear models (total winter range: $\Delta AIC_c = 1·70$; park winter range: $\Delta AIC_c = 0·65$). However, the shape of the relationship described by these models was concave down, indicating that the relative frequency of bison attacks *decreased* with relative bison abundance. This negatively frequency-dependent pattern is opposite of that predicted by the switching hypothesis.

Fitting a nonlinear model of Murdoch's (1969) modified equation to the kill data similarly revealed no evidence of prey switching. This model suggested that wolves maintained a strong aversion to killing bison in the total winter range (c = 0·04 [95% CI = −0·10, 0·17]) and park winter range (c = 0·001 [−0·005, 0·007]) that seemed to strengthen as relative bison abundance increased: b = 0·74 [0·12, 1·35] (total winter range), b = 0·47 [0·10, 0·84] (park winter range). The curvilinear, concave-down relationship described by these models (Fig. 3c,d) also indicates negatively frequency-dependent predation. This pattern is particularly strong in the park winter range where the 95% CI for the switching variable b excludes 1.

WOLF–BISON BEHAVIOURAL INTERACTIONS

We obtained detailed behavioural data for 187 wolf–bison encounters; 74 (40%) included ≥1 attack (mean ± SE = 0·93 ± 0·20 attacks/encounter; range = 0–26) and 11 (6%) included ≥1 capture (mean ± SE = 0·13 ± 0·12 captures/encounter; range = 0–5). These encounters included a total of 173 attacks, 24 captures and 8 kills.

Mixed groups were less aggressive than bull groups when wolves attacked: they were less likely to charge (odds ratio, OR [95% CI] = 0·33 [0·16, 0·69], P = 0·003) and more likely to flee (OR = 3·89 [1·19, 12·68], P = 0·02). Bison were also more likely to flee as the number of wolves attacking increased (OR = 1·24 [1·10, 1·41], P < 0·001).

Attack probability decreased linearly with bison group size (OR = 0·94 [0·90, 0·99], P = 0·02; Fig. 4a); a nonlinear effect of bison group size did not improve model fit ($\chi^2_1 = 0·20$, P = 0·65). Wolves were more likely to attack mixed groups than bull groups (OR = 6·24 [1·33, 29·33], P = 0·02) and bison that fled vs. those that stood their ground (OR = 10·38 [2·70, 39·97], P = 0·001).

The effect of bison group size on capturing was nonlinear; a cubic transformation of bison group size outperformed the simple linear effect ($\chi^2_1 = 7·23$, P = 0·007). Capture probability increased with group size up to about 15 bison (β_1 = 0·51 [0·05, 0·96], P = 0·03) after which it declined (β_2 = −4·81 [−9·00, −0·63], P = 0·02). Wolves were most likely to capture bison when they attacked groups numbering between about 10–20 animals (Fig. 4b). Wolves were also more likely to capture bison in groups that fled vs. those that confronted them (OR = 7·83 [1·73, 35·49], P = 0·008). Bison group composition (bulls vs. mixed group) had no apparent effect on capture probability (OR = 0·97 [0·14, 6·53], P = 0·97). However, once wolves targeted an individual bison, they were more likely to capture a calf than a bull (OR = 17·79 [3·83, 82·56], P < 0·001) or a cow (OR = 11·15 [2·01, 62·00], P = 0·006); capture probability did not differ between cows and bulls (OR = 1·60 [0·37, 6·96], P = 0·53).

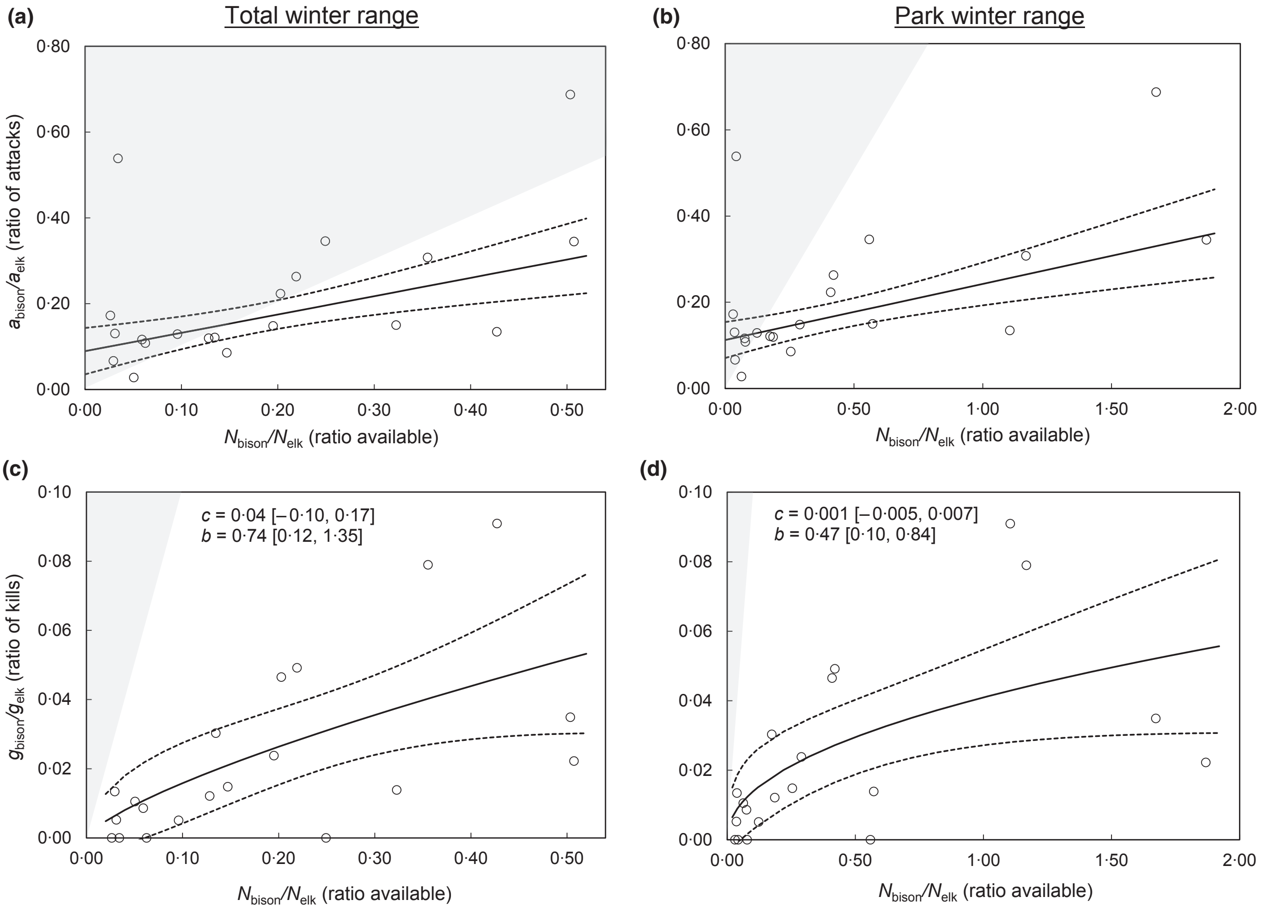

Fig. 3. Effects of relative bison abundance on the relative frequency that wolves attacked (a, b) and killed (c, d) bison in the total (a, c) and park (b, d) winter ranges. Solid lines are fitted values with dotted lines indicating 95% confidence intervals. Open circles are observed annual ratios ($N = 20$). Shaded areas are the parameter spaces indicative of preference for bison. The dividing lines between shaded and non-shaded areas indicate values where the relative frequency of attacks and kills is exactly proportional to relative bison abundance.

Sensitivity scores suggest that attack probability was most influenced by wolf group size (0·008), followed by bison flight response (0·005), bison group composition (0·004) and bison group size (0·001) (Fig. 4c). Capture probability was most influenced by bison group size (0·15), flight response (0·05), wolf group size (0·03) and bison group composition (0·001) (Fig. 4d).

BISON SCAVENGING

Wolf use of bison carrion increased during 1995–2015 ($r^2 = 0.64$; range = 0–20; Fig. 5a), and was well-correlated with bison abundance ($r^2 = 0.71$; Fig. 5b). There was evidence that high levels of bison scavenging depressed bison attack and kill frequencies. A nonlinear effect of bison scavenging fitted these data as well as or better than did a linear effect (attacking: $\Delta\text{AIC}_c = 0.23$; killing: $\Delta\text{AIC}_c = 0.00$; Fig. 5c,d).

Discussion

Identifying the biological mechanisms that promote the stability of multi-prey systems is a long-standing goal in ecology (May 1972; Valdovinos *et al.* 2010). Prey switching behaviour is one of the most venerable of these mechanisms (Murdoch 1969); one that has found wide use in models of predator–prey interactions (e.g. Varley & Boyce 2006; Valdovinos *et al.* 2010; van Leeuwen *et al.* 2013; Morozov & Petrovskii 2013). It is frequently invoked to justify a stabilizing Type III functional response (Holling 1959). However, empirical studies of switching behaviour in free-living multi-prey systems are rare and seldom clarify the underlying mechanisms that drive patterns in prey preference. Our study provides one of the first comprehensive tests of the switching hypothesis in a large-scale, free-living predator–prey system. An important feature of this natural system, like many others, is that prey species were not uniformly vulnerable to predation; some species were more dangerous than others.

In the northern Yellowstone wolf–elk–bison system we studied, the predator (wolves) maintained a strong preference for the safer prey species (elk). Contrary to the switching hypothesis, this preference did not weaken as the relative abundance of the safer prey species decreased. Likewise, preference for the more dangerous prey species (bison) did not strengthen as the relative abundance of this species increased. We obtained the same results regardless

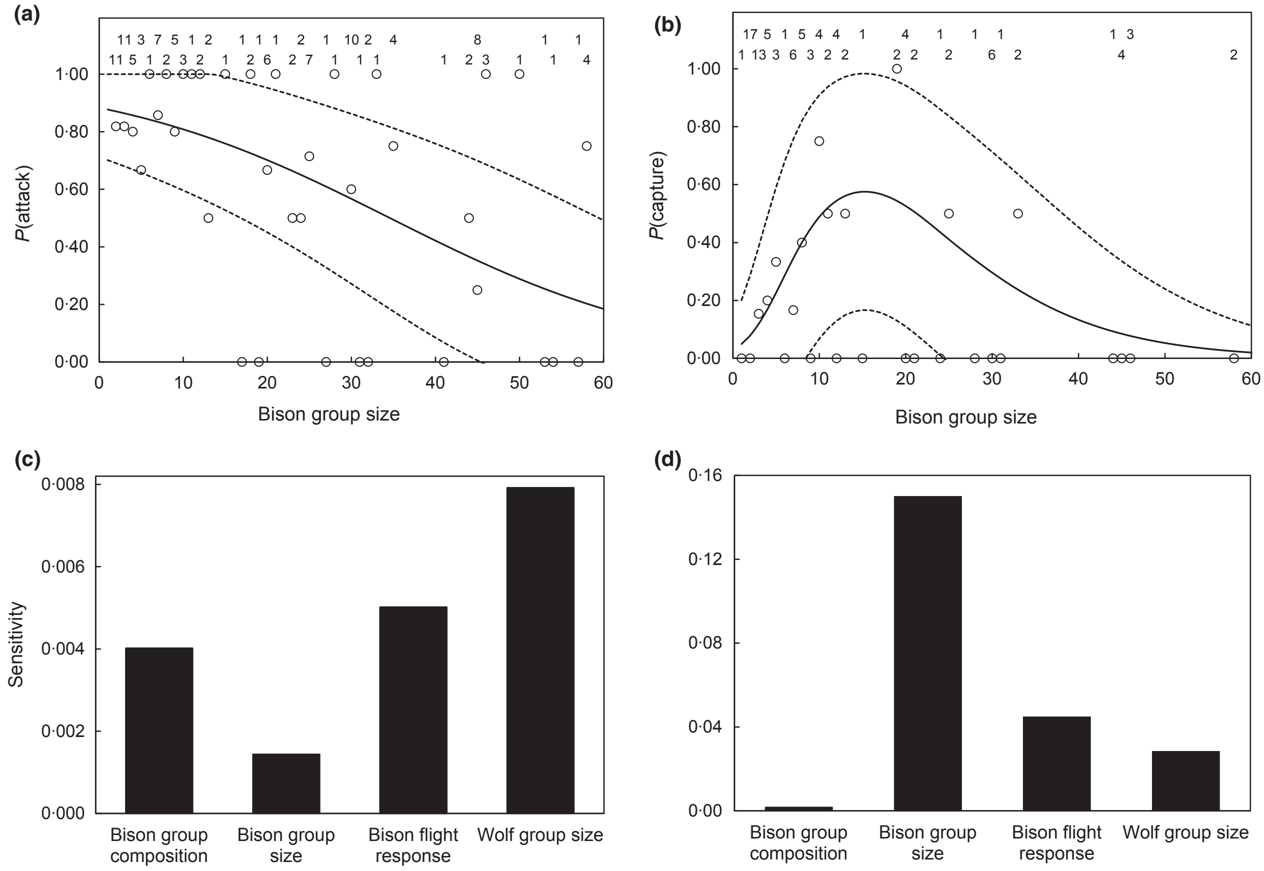

Fig. 4. Effects of bison group size on the probability of attacking (a) and capturing (b) and the relative influence of bison group composition and size, flight response and wolf group size on attacking (c) and capturing (d). In (a) and (b), lines are population-averaged fitted values with associated 95% confidence intervals, and open circles are observed frequencies with sample sizes denoted above each point; analyses were performed on the raw binary data and not the illustrated data points. The number of wolf–bison encounters included in each analysis is 171 (a, c) and 91 (b, d). Each bar in (c) and (d) represents a sensitivity value generated by taking the difference between initial and perturbed (10%) predicted values for each parameter. The greater the sensitivity value, the more influential that parameter is on attack and capture probability.

of whether we defined the study system as the entire northern Yellowstone elk winter range, or only that portion of the winter range inside Yellowstone where elk abundance was lowest. Results were also consistent across two separate measures of predator preference. The first involved direct behavioural observations of wolves encountering and attacking each prey species, and the second involved identification of remains from wolf-killed prey.

Overall, our results indicate that wolves maintained a strong and constant aversion to attacking and killing bison across a range of relative abundance ratios that varied from one bison per 35 elk to nearly two bison per elk. [Correction added after online publication on 26 April 2017: 'more than' changed to 'nearly']. These findings are consistent with similar analyses of wolves, elk and bison in the Madison headwaters region of central Yellowstone (Becker *et al.* 2009). Wolves in the Mackenzie Bison Sanctuary, Canada, similarly avoided bison in favour of safer prey (moose), even though bison were more numerous (Larter, Sinclair & Gates 1994). In northern Yellowstone, there was some evidence that wolf aversion to bison actually strengthened as the relative abundance of bison increased. This was most apparent in the analysis of kill ratios inside the park (Fig. 3d). In this case, $b < 1$ ($b = 0{\cdot}47$, 95% CI = 0·10–0·84) implies a decreasing preference for bison and an increasing preference for elk as the ratio of bison to elk increased. We detected a similar but weaker pattern when this analysis included the area outside Yellowstone ($b = 0{\cdot}74$, 95% CI = 0·12–1·35; Fig. 3c).

Results from the attack ratio analysis provide additional support for this pattern. At low relative bison abundance, most of the observed attack ratios were more than proportional to relative bison abundance, whereas at high relative bison abundance, most of the observed attack ratios were less than proportional to relative bison abundance. This pattern was the same when calculated across both the total and park winter range. This implies that wolves preferred attacking bison when they were relatively rare, but avoided attacking them when they were relatively abundant. A nonlinear relationship between attack ratio and relative abundance described the data nearly as well as a linear relationship ($\Delta\text{AIC} \leq 1{\cdot}70$) when two outliers were excluded

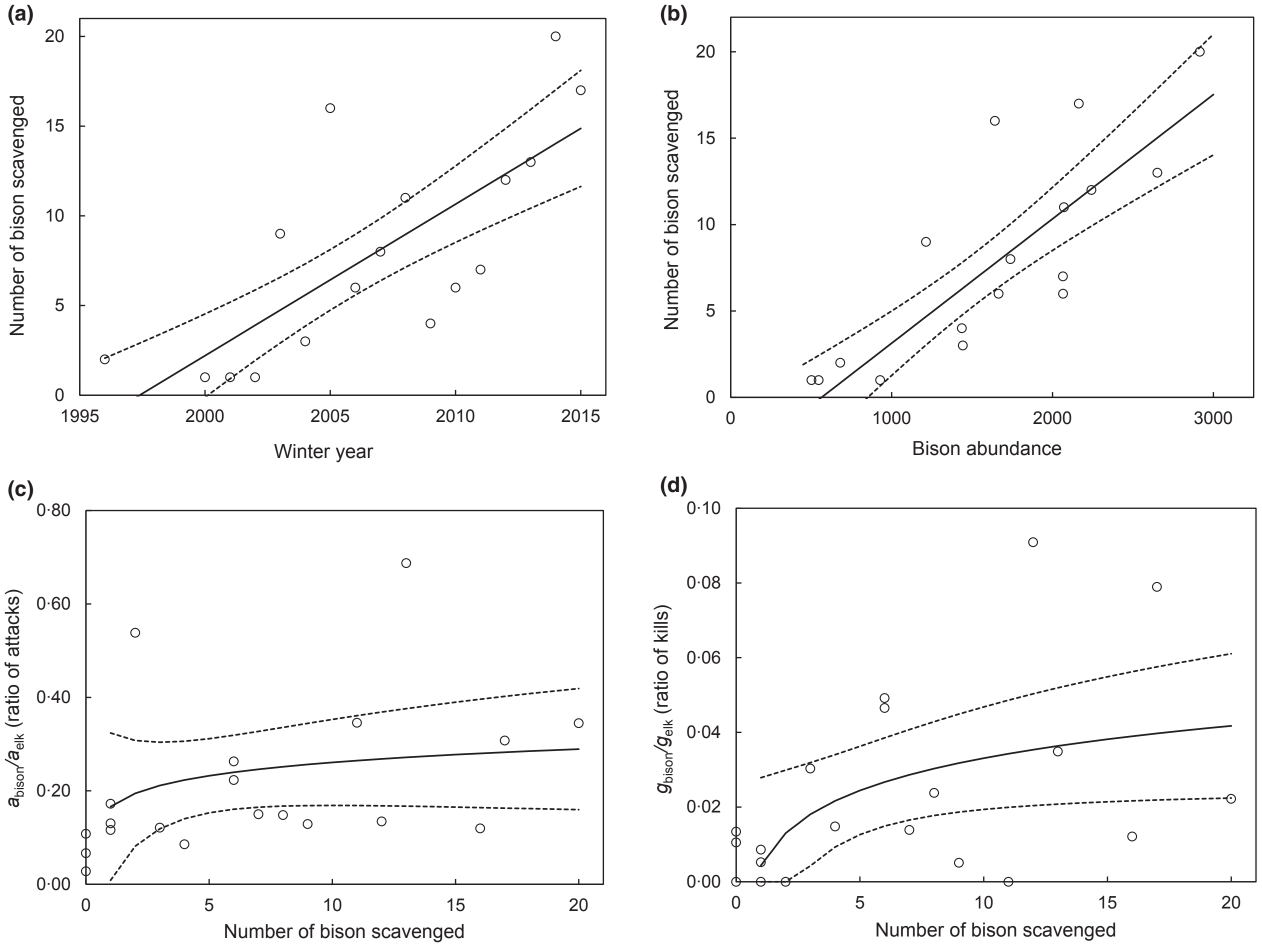

Fig. 5. Number of wolf-scavenged bison in the northern Yellowstone National Park winter range, 1995–2015, (a) in relation to bison abundance (b), and the relative frequency that wolves attacked (c) and killed (d) bison. Open circles are observed values and solid lines are fitted values with dotted lines indicating 95% confidence intervals.

from the analysis, providing additional support for this pattern. Taken together, our results suggest that wolf predation on bison in northern Yellowstone was potentially negatively frequency dependent, contrary to the positively frequency-dependent predation predicted by the switching hypothesis.

Strong preference against attacking and killing bison was a fundamental consequence of the inability of wolves to consistently overcome bison antipredator defences. Less than 5% of 187 directly observed wolf–bison interactions resulted in a kill. This is consistent with previous research indicating that bison are the most difficult ungulate prey for wolves to kill in North America (Carbyn, Oosenbrug & Anions 1993; Mech & Peterson 2003; Mech, Smith & MacNulty 2015). Our behavioural analysis indicates this is because the ability of wolves to kill bison was limited to a narrow range of conditions, characterized by small mixed groups of bison (10–20 animals; Fig. 4b) fleeing from large groups of wolves (>11 wolves; MacNulty *et al.* 2014). These results are broadly consistent with observations of wolves hunting bison in Wood Buffalo National Park, Canada, which is the only other wolf–bison system where comparable behavioural data are available (Carbyn & Trottier 1987, 1988; Carbyn, Oosenbrug & Anions 1993).

A unique aspect of our study is that we quantified the influence of predator and prey traits on the success of wolves hunting bison. We found that herds with >20 bison were effective at repelling wolves, which accords with a general understanding of the antipredator benefits of grouping (Krause & Ruxton 2002; Caro 2005). On the other hand, we also found that wolves were less likely to capture a bison as herd size dropped below about 10 animals (Fig. 4b). Similar nonlinear effects of ungulate group size on predator success have been documented in other wolf populations (Hebblewhite & Pletscher 2002) and carnivore species (Creel & Creel 2002). Predators that hunt dangerous prey depend on individuals that are either young, old or in poor body condition (Temple 1987; Carbyn, Oosenbrug & Anions 1993; Wright *et al.* 2001), which are typically rare in any given prey population (Hamilton 1971). The ability of wolves to capture bison calves, together with the tendency of bison calves to aggregate in large mixed age–sex groups, suggests that the ascending limb of the of the curve in Fig. 4b reflects an increased likelihood of finding a calf as herd size increases.

Our sensitivity analysis revealed that bison group size had the strongest influence on wolf capture success compared to wolf group size, bison flight response and bison group composition (Fig. 4d). By contrast, wolf group size was the best predictor of the probability of attack, followed by bison flight response, group composition and group size (Fig. 4c). Previous work has shown that the probability of attacking and capturing bison increases with wolf group size (MacNulty *et al.* 2014). Our results suggest that larger packs may be more likely to attack bison because they are better able to provoke a flight response. Similarly, wolves probably attacked mixed groups more often than bull groups, in part, because the former fled more often than the latter. Flight response was the second best predictor of attacking and capturing, which aligns with findings from other studies that demonstrate the importance of ungulate flight response to carnivore hunting success (Lingle & Pellis 2002; Caro 2005).

The difficulty of hunting bison, together with the availability of bison carrion, encouraged wolves to scavenge dead bison rather than attack live ones. The ability of wolves to shift from hunting to scavenging as bison abundance increased (Fig. 5) is one reason why wolf predation on bison could be negatively frequency dependent. Increased availability of bison carrion with bison population size (Reagan 2016) may have reduced the incentive to attack bison when they were relatively abundant. By 2014, wolves acquired nearly as much biomass from scavenged bison as they did from hunted elk (Metz *et al.* 2016). Thus, one potential outcome of an increasing population of dangerous prey is that predators shift foraging strategies (e.g. hunting to scavenging) rather than shift prey preference.

The consequences of shifting foraging strategies for the dynamics of a preferred, safer prey species (e.g. elk) depend on the predator's numerical response (Moléon *et al.* 2014). For example, if the carrion of dangerous prey boosts predator numbers, it could increase predation pressure on the safer prey if the proportional increase in predator numbers exceeds the proportional decrease in per capita intake of safer prey. Alternatively, increased carrion availability could decrease predation pressure on the safer prey, provided that predator numerical responses to carrion availability do not compensate for lower individual predation rate (Moléon *et al.* 2014). Wolf numbers in northern Yellowstone have decreased as bison numbers increased (Smith *et al.* 2016), implying a lack of numerical response. Thus, wolf scavenging on bison may divert predation away from elk, helping to stabilize wolf–elk interactions.

In conclusion, our results suggest that prey switching is an unlikely stabilizing mechanism in predator–prey systems where the alternative prey is dangerous. This is because the potentially severe fitness costs of attacking dangerous prey (e.g. injury or death) causes predator preference for different prey species to vary in relation to relative prey vulnerability, which is ultimately a function of the predator and prey traits that determine the outcome of interactions. Moreover, predators may respond to the rise of a dangerous prey species by shifting foraging strategies not prey preferences. This is a departure from classic theory which maintains that prey preference is primarily a function of relative prey abundance (Murdoch 1969; Murdoch & Oaten 1975). This is important for understanding the dynamics of dangerous prey systems because incorrectly assuming prey switching overestimates the stability of ecological communities (van Leeuwen *et al.* 2013). We encourage future studies of dangerous prey systems to explore alternative stabilizing mechanisms, including facultative shifts between hunting and scavenging.

Authors' contributions

A.T. and D.M. conceived of the study and led the writing of the manuscript; A.T., C.G., C.T.W., D.M., D.R.S., D.W.S., J.R., M.M., R.W. participated in data collection; A.T., D.M., J.R. carried out statistical analyses; C.G., D.R.S., D.W.S., R.W. coordinated the long-term study in Yellowstone National Park. All authors approved of this publication.

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Data accessibility

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.h5486 (Tallian *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Estimating elk abundance.

Table S1. Number of elk counted in the total and park winter ranges during annual winter aerial surveys in northern Yellowstone.

SUPPORTING INFORMATION

Appendix S1. Estimating elk abundance

First, we used a state-space model constructed from uncorrected elk counts to interpolate elk counts for years in which no survey occurred (1996, 1997, 2006, and 2014). State-space models can, in some cases, separate process error (i.e., variation arising from ecological processes) from observation error (i.e., variation arising from imperfect sampling) which makes this an appealing method when dealing with imprecise count data (de Valpine & Hastings 2002; Buckland *et al*. 2004; Clark & Bjornstad 2004). The interpolated count is conditional on the full time series of data and constrained by a population growth model (Clark & Bjornstad 2004). We used a state-space formulation of the Gompertz population growth model because it accurately portrays density-dependent population growth (Dennis *et al*. 2006). Although state-space models can be implemented using both Bayesian and likelihood approaches, we opted to use a Bayesian approach because of the ease in which it handles missing data (Kéry & Schaub 2012).

Gompertz population growth model - We specified that the true population size at time t (N_t) was a function of the population size in the previous year (N_{t-1}) multiplied by growth rate, which is the exponential of $\beta_0 + \beta_1 * \log(N_{t-1})$ in a Gompertz model (equation 1). Here, β_0 is equivalent to r_{max}, i.e., the maximum growth rate that a given species' population could attain at a low population density. β_1 estimates the strength of density dependence, i.e., the degree to which r_{max} is influenced by population density. $\beta_1 < 0$ indicates that population growth rate is less than r_{max} as population size increases. By taking the logarithm of both sides of equation 1, a simple additive linear model is obtained (equation 2), where $x_t = \log(N_t)$. For brevity, we refer to the Gompertz equation as $f(x_{t-1})$.

$$\text{Equation 1: } N_t = N_{t-1} * e^{(\beta_0 + \beta_1 * \log(N_{t-1}))}$$

$$\text{Equation 2: } x_t = x_{t-1} + \beta_0 + \beta_1 * x_{t-1} = f(x_{t-1})$$

State-space model - To represent the Gompertz equation as a state-space model, we linked the process model (equation 2) to an observation model in order to separate process error (σ_p^2) from observation error (σ_o^2). This is achieved through the following set of equations

$$\text{Equation 3: } x_t = f(x_{t-1}) + \varepsilon_t$$

$$\text{Equation 4: } y_t = g(x_t) + w_t$$

in which equation 3 is the process (i.e., Gompertz) model from above, with a normally distributed error term [$\varepsilon_t \sim N(0, \sigma_p^2)$] which accounts for variation not explained by the Gompertz model. In equation 4, y_t is the log number of observed elk during each survey, and it is linked to the underlying state by the observation model $g(x_t)$and a normally distributed error term [$w_t \sim N(0, \sigma_o^2)$] to account for observation error.

In Bayesian analyses, prior distributions must be provided for all random variables. We chose vague priors for variables for which we had no prior data, namely σ_p^2 and σ_o^2. We provided more informative priors for parameters which could be reliably estimated from ecological theory, i.e., β_0 and β_1. Providing informative priors in cases when it is appropriate results in greater identifiability of other model parameters, including process and observation errors (Lebreton & Gimenez 2013). Following Koons *et al*. (2015), we estimated an informative Gaussian prior distribution for β_0 ($\bar{x} = 0.263$, $SD = 0.09$) from estimates of $r_{\max}$ in elk (Caughley 1977; Houston 1982; Hennemann 1983; Eberhardt 1987; Gogan & Barrett 1987; McCorquodale, Eberhardt &

Eberhardt 1988) summarized in Duncan, Forsyth & Hone (2007) and defined a zero mean Gaussian prior distribution for β_1 truncated at -2, 2.

The full model, including prior distributions, is:

$$\mathrm{P}\left[\boldsymbol{x}, \boldsymbol{\beta}, \sigma_{\mathrm{p}}^2, \sigma_{\mathrm{o}}^2 \,\middle|\, \boldsymbol{y}\right] \propto$$

Process model:

$$\prod_{t=2}^{T} \mathrm{Normal}\left(x_{\mathrm{t}} \middle| f\ (x_{\mathrm{t}-1};\ \boldsymbol{\beta}),\ \sigma_{\mathrm{p}}^2\right) \times$$

Observation model:

$$\prod_{t=1}^{T} \mathrm{Normal}(y_t | g(x_{\mathrm{t}}),\ \sigma_{\mathrm{o}}^2) \times$$

Parameter models:

$$\text{Inverse Gamma}\left(\sigma_{\mathrm{p}}^2 | 0.001, 0.001\right) \times$$

$$\text{Inverse Gamma}(\sigma_{\mathrm{o}}^2 | 0.001, 0.001) \times$$

$$\mathrm{Normal}(\beta_0 | 0.263, 0.09^2) \times$$

$$\mathrm{Normal}(\beta_1 | 0, 2^2)\mathrm{T}(-2, 2)$$

Model implementation - We conducted Markov Chain Monte Carlo (MCMC) simulations in JAGS (v. 3.4.0; Plummer 2012) via Program R and the R2jags package (Su & Yajima 2012) to estimate posterior distributions of the parameters of interest. For each model, we ran three chains each consisting of 100,000 iterations with the first 50,000 discarded as burn-in, and thinned the sample to retain every 50th simulation. Model convergence was assessed visually using trace plots and by ensuring each parameter of interest had a $\hat{R}$ value < 1.05 (Gelman 1996). We assessed model goodness-of-fit using posterior predictive checks (Gelman *et al*. 2004; Kéry & Schaub 2012; Hobbs & Hooten 2015; Hooten & Hobbs 2015). To achieve this, we generated hypothetical count data (i.e., $Y.new_t$) from the model and used a squared discrepancy statistic to compare observed and expected values from the original and new datasets at every MCMC iteration, i.e., $(Y_t - N_t)^2$ and $(Y.new_t - N_t)^2$. Calculating the proportion of iterations in which the discrepancy statistics arising from the original and hypothetical datasets were more extreme than one another provided a measure of goodness-of-fit; a value of 0.5 indicates perfect fit, while values close to 0 or 1 indicate lack of fit.

Sightability model – Finally, we used a modified version of the Singer and Garton (1994) northern Yellowstone elk sightability model to adjust counts for imperfect detection. We used Singer and Garton's (1994) sightability data to estimate a reduced version of their model that included group size as the sole covariate. A reduced model was necessary because aerial survey data were insufficient to estimate their model's other effects, which included vegetation cover and elk activity. We estimated the following logistic regression model which predicted that the probability of sighting elk increased with elk group size:

Parameter	β	SE	*z*	*P*	95% confidence interval for β	
Intercept	-0.5525	0.2411	-2.29	0.022	-1.025	-0.080
Group size	0.0487	0.0131	3.72	<0.001	0.023	0.073

We divided the group size of each counted group by its predicted sightability and summed these values to estimate a corrected count for each survey. We corrected surveys lacking group size data by applying an average sightability estimated from adjacent years. We counted elk as inside or outside the park using the geographic coordinates assigned to each sighted group. In years when such detailed location data were unavailable, we estimated the numbers of elk inside the park by multiplying the total corrected count by the average proportion of elk inside the park during adjacent years.

SUPPLEMENTARY TABLE

Table S1. Number of elk counted in the total and park winter ranges during annual winter aerial surveys in northern Yellowstone. Interpolated elk counts from the state-space model for years when no survey occurred are in **bold**. Sightability corrected counts for the total and park elk winter ranges, which were used for analysis, are in *italics*.

Year	Survey Date	Total Elk Count	Park Elk Count	Corrected Total Elk Count	Corrected Park Elk Count
1995	12/21/1994	16791	13097	*22189*	*17740*
1996	NA	**15062**	**11748**	*19904*	*15913*
1997	NA	**13459**	**10498**	*17786*	*14219*
1998	1/18/1998, 1/27/1998	11736	9137	*15509*	*12376*
1999	1/30/1998, 2/11/1999	11742	8807	*15517*	*11928*
2000	12/27/1999	14539	10904	*19106*	*16372*
2001	12/21/2000	13400	10050	*17609*	*15089*
2002	12/21-23/2001	11969	8446	*15729*	*12278*
2003	12/24/2002	9215	6759	*12662*	*9846*
2004	12/18/2003	8335	6094	*10724*	*8275*
2005	1/5/2005	9545	6175	*12808*	*8831*
2006	NA	**7992**	**3405**	*10192*	*5045*
2007	12/30/2006	6738	4331	*8913*	*5997*
2008	2/14/2008	6279	2281	*8309*	*3701*
2009	1/30/2009, 2/9/2009	7109	3576	*9771*	*5643*
2010	2/26/2010	6070	2698	*7601*	*3959*
2011	12/21/2010	4635	2399	*6398*	*3609*
2012	3/7/2012	4174	1440	*5248*	*2029*
2013	2/18/2013	3915	915	*5268*	*1585*
2014	NA	**4400**	**1012**	*5749*	*1561*
2015	1/20/2015	4844	1130	*6090*	*1853*

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