

Strategy, compromise, and cheating in predator–prey games

Nicholas Wolf† and Marc Mangel*

*Center for Stock Assessment Research and Department of Applied Mathematics and Statistics,
MS E2, University of California, Santa Cruz, CA 95064, USA*

ABSTRACT

Background: A prey's optimal level of anti-predator behaviour depends on its hunger state and its assessment of danger in the environment. Similarly, a predator's optimal attack behaviour depends on its own satiation level and its assessment of the risks and costs associated with hunting. The optimal behaviour of each depends on what the other is doing, resulting in a dynamic game.

Assumptions: We assume that predators are more successful at hunting their prey when prey are further from safety, and that prey are more successful in finding their food items in more risky environments.

Question: Under these assumptions, what is the evolutionarily stable strategy (ESS) and how does it respond to false attacks by the predators?

Mathematical methods: We use stochastic dynamic programming to compute the probabilities of prey and predators surviving a foraging season (e.g. the winter) and game theoretical methods to compute the evolutionarily stable strategies.

Results: We find the ESS, and we demonstrate that when foraging time is limited, a predator benefits from making extra 'false' attacks on the prey, assuming it can do so safely and efficiently. The extra attacks disturb the prey until they can no longer afford the time for anti-predator behaviour and become easier targets during the next 'real' attack.

Keywords: evolutionarily stable strategies, game theory, killer whale, krill, Steller sea lions, stochastic dynamic programming.

INTRODUCTION

Many organisms buffer against the risk of predation by investing in stealth or vigilance or by moving into safer but less profitable patches (Lima and Dill, 1990). When successful, these anti-predator behaviours reduce the risk of capture to the point where the predator's only impact on the prey is in terms of lost foraging or reproductive opportunities. Such a system could be described as 'danger-driven', as opposed to 'mortality-driven', in which death

* Author to whom all correspondence should be addressed. e-mail: msmangel@ucsc.edu

† Present address: Akeena Solar, 16005 Los Gatos Boulevard, Los Gatos, CA 95032, USA.

Consult the copyright statement on the inside front cover for non-commercial copying policies.

is the primary fitness consequence of predation risk [Brown *et al.* (1999); their terms were ‘ μ -driven’ and ‘ N -driven’].

Most predator–prey interactions fall somewhere in between these two extremes: Prey sacrifice certain opportunities but still accept some reduced level of risk. The resulting trade-off between safety and foraging or reproductive opportunities has been investigated by many researchers using optimality models (e.g. Rands and Cuthill, 2001; McNamara *et al.*, 2005; Polo *et al.*, 2005; Frid *et al.*, 2006).

Predator and prey behaviours are adaptively linked as a result of co-evolution, and the effectiveness of an anti-predatory response depends in part on the extent to which it modifies predator behaviour (and vice versa). This interaction implies an ecological behavioural game played out over evolutionary time. In contrast with spatial games, which have received considerable attention (reviewed in, for example, Lima, 2002), behavioural games between predator and prey have only rarely been examined (but see Bouskila *et al.*, 1998; Brown *et al.*, 2001; Hugie, 2003). In this paper, we develop such a behavioural game and reveal a novel aspect of the interaction.

Our work is motivated by studies of the transient killer whale, *Orcinus orca*, which hunts (among other things) Steller sea lions, *Eumetopias jubatus*, in western Alaska (Mangel and Wolf, 2006; Wolf *et al.*, 2006). The well-studied but still poorly understood decline of the Steller sea lion was probably the result of multiple factors, including killer whale predation (Guenette *et al.*, 2006; Wolf *et al.*, 2006; N. Wolf and M. Mangel, submitted). However, examples abound. For example, southern ocean krill (*Euphausia superba*) are involved in similar predator–prey games with diving mammals and birds (Alonzo and Mangel, 2001; Alonzo *et al.*, 2003). Krill migrate between the surface and great depths in the water column. Close to the surface food is abundant, but so are predators [which may once have been at depth too (see Willis, 2007)]. Predators, such as penguins, seals, and some whales, can most effectively prey on krill at the surface where food is most abundant.

To help focus discussion, we shall use Steller sea lions and killer whales as a heuristic description, and presume that the reader (in a kind of ‘choose your own adventure’) will insert a favourite predator–prey system. In the model, natural selection acts on the attack rate of killer whales and the foraging location (distance from the haulout) of sea lions. Fitness for both players in the game is the probability of surviving the winter, when food limitation is an issue.

DETAILS AND METHODS

Killer whales

Killer whales probably rely upon the element of surprise when hunting sea lions (Barrett-Lennard *et al.*, 1996). In the event of an attack, a sea lion’s best defence is to flee to the nearest haulout and climb out of the water. Therefore, the probability of capture in the event of an attack should increase with distance from the haulout. We use an exponential function (Fig. 1) to define capture probability per attack, $\mu(d)$, as a function of distance from the haulout, d :

$$\mu(d) = \mu_{\max} \left[1 - \left(\frac{1}{2} \right)^{\frac{d}{c_{\mu}}} \right], \quad (1)$$

where c_{μ} is a constant equal to the distance at which the capture probability is 1/2 of its maximum value, $\mu_{\max}$.

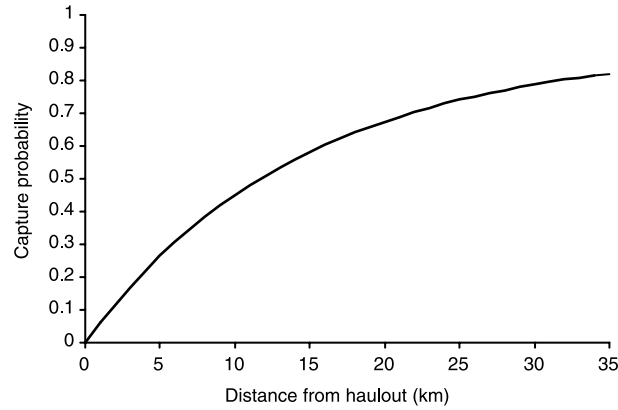


Fig. 1. Capture probability as a function of distance from the haulout.

If attacks are randomly distributed in time, the probability that a killer whale fails to capture any prey all day, P_K , is the Poisson probability of zero successes (Mangel, 2006) with a rate of $\mu(d)aq$, where a is the attack rate and q is the length of the day:

$$P_K(a, d) = e^{-\mu(d)aq}. \quad (2)$$

A string of unsuccessful days can lead to starvation. The fasting interval, f_K , is the maximum number of consecutive days that a killer whale can survive without catching any prey. We use the function $W_K(x, t, a, d, f_K, T)$ to denote the probability that an individual killer whale survives to the end of a winter season of length T without experiencing any shortfalls exceeding f_K in length, starting at date t with hunger state x (days since last meal). This function has no analytical solution, but we can calculate it without difficulty using backward iteration (Mangel and Clark, 1988; Clark and Mangel, 2000) analogous to stochastic dynamic programming:

$$W_K(x, t, a, d, f_K, T) = P_K(a, d) \begin{cases} W_K(x+1, t+1, a, d, f_K, T) & \text{if } x+1 \leq f_K \\ 0 & \text{if } x+1 > f_K \end{cases} + (1 - P_K(a, d))W_K(0, t+1, a, d, f_K, T). \quad (3)$$

The calculation begins at the end of the season, when $W_K(x, t, a, d, f_K, T) = 1$ for all $x \leq f_K$ and $= 0$ otherwise, and moves backward through time until it arrives at $t = 1$, at which point the probability of surviving from the beginning to the end of the season is given by $W_K(0, 1, a, d, f_K, T)$.

Killer whales also face a small risk of mortal injury per attack, i , and the Poisson probability of avoiding death due to injury is e^{-aiqT} . The winter survival probability for a killer whale (our proxy for fitness) is, therefore,

$$F_K(a, d) = W_K(0, 1, a, d, f_K, T)e^{-aiqT}. \quad (4)$$

Sea lions

As described above, we assume that foraging conditions for the sea lions are better further from the haulout (due to local depletion), so that the animals are faced with a trade-off

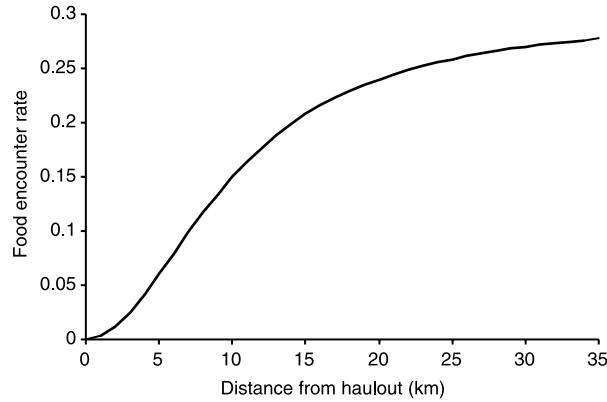


Fig. 2. Food encounter rate (for sea lions) as a function of distance from the haulout.

between the hazards of starvation and predation. We model food encounter rate for sea lions, $Y(d)$, as a function of distance from the haulout using a Holling Type 3 functional response (Holling, 1959) (Fig. 2):

$$Y(d) = Y_{\max} \left(\frac{d^2}{d^2 + c_Y^2} \right) \quad (5)$$

where c_Y is a constant reflecting the distance at which the encounter rate is half of the maximum value, $Y_{\max}$.

Attacks by killer whales disturb the sea lions and prevent foraging for a period of h hours, so that the average amount of time available each day for foraging is $q - aqh$ hours. The Poisson probability that a sea lion fails to catch any prey all day is therefore approximately

$$P_S(a, d) = e^{-Y(d)(q - aqh)}. \quad (6)$$

Sea lions are also assumed to starve if they do not find food by the end of their maximum fasting interval, f_S . The probability of a sea lion surviving through winter (starting at date t with hunger state x) without experiencing any fatal shortfalls is similarly defined as the function $W_S(x, t, a, d, f_S, T)$, again calculated using backward iteration:

$$W_S(x, t, a, d, f_S, T) = P_S(a, d) \begin{cases} W_S(x+1, t+1, a, d, f_S, T) & \text{if } x+1 \leq f_S \\ 0 & \text{if } x+1 > f_S \end{cases} + (1 - P_S(a, d)) W_S(0, t+1, a, d, f_S, T). \quad (7)$$

The probability of avoiding predation for the whole season is $e^{-ar\mu(d)qT}$, where r is the ratio of predators to prey (Hilborn and Mangel, 1997). Sea lion fitness (the probability of winter survival) is, therefore,

$$F_S(a, d) = W_S(0, 1, a, d, f_S, T) e^{-ar\mu(d)qT}. \quad (8)$$

The parameter values used in the model are listed in Table 1. Although none are estimated from empirical data, these values are both representative and plausible. Minor variation in the parameter values does not affect the model's qualitative results.

Table 1. Parameter values used in the model

Parameter	Value
Season duration (days)	$T = 180$
Number of hours available each day for hunting/foraging	$q = 12$
Maximum fasting period (days) for killer whales	$f_K = 12$
Maximum prey capture probability in attacks far from the haulout	$\mu_{\max} = 0.9$
Distance from haulout (km) where $\mu = \mu_{\max}/2$	$c_{\mu} = 10$
Probability of mortal injury for killer whales per attack	$i = 0.001$
Ratio of predators to prey	$r = 0.05$
Maximum fasting period (days) for sea lions	$f_S = 6$
Maximum food encounter rate (per hour) for sea lions far from the haulout	$Y_{\max} = 0.3$
Distance from haulout (km) where $Y = Y_{\max}/2$	$c_Y = 10$
Foraging time (hours) lost by all sea lions due to each attack	$h = 2$

RESULTS

Figures 3 and 4 show the fitness surfaces for killer whales and sea lions at the start of winter. In Fig. 3, the dotted line (connecting vertical tangents of the fitness contours) corresponds to a killer whale's optimal attack rate strategy in response to the foraging distance used by sea lions. The predator's optimal strategy is to avoid unnecessary risk and decrease its attack rate when the prey are more vulnerable (further from the haulout). The dotted line in Fig. 4 similarly corresponds to a sea lion's optimal foraging strategy (distance from the haulout) in response to the attack rate chosen by killer whales. The line is U-shaped, reflecting a shifting trade-off between predation and starvation risk: At low attack rates, sea lions go where the food is, far from the haulout. At intermediate attack rates, the risk of predation drives them closer to the safety of the haulout. At high attack rates, so much foraging time is lost due to attacks that the animals must forage further out again to avoid starvation.

By choosing to forage in a more dangerous area, the sea lions are effectively reducing their level of anti-predator behaviour in response to elevated attack rates. This counter-intuitive result is actually quite general. We should expect reduced anti-predator behaviour in any situation where: (1) foraging time is limited, (2) predator attacks are frequent, and (3) foraging is interrupted by each attack. The same mechanism might explain Lima's (1986) observation of house sparrows decreasing vigilance in apparently dangerous settings.

The two response curves form the basis of a game played out over evolutionary time-scales (Fig. 5): Given a population of sea lions using a fixed foraging strategy (distance from the haulout), killer whales are predicted to evolve towards the corresponding attack strategy (rate) shown by the dashed line. Given that attack rate, the sea lions are predicted to evolve towards the corresponding foraging strategy (distance from the haulout) shown by the dotted line. In further iterations, the system eventually converges towards the stable point at the intersection of the two lines. This is a Nash equilibrium (Nash, 1950; Clark and Mangel, 2000).

Manipulating prey behaviour

When considering the game detailed in Fig. 5, one might ask what would happen if the predator were somehow able to make additional 'false attacks' without incurring the

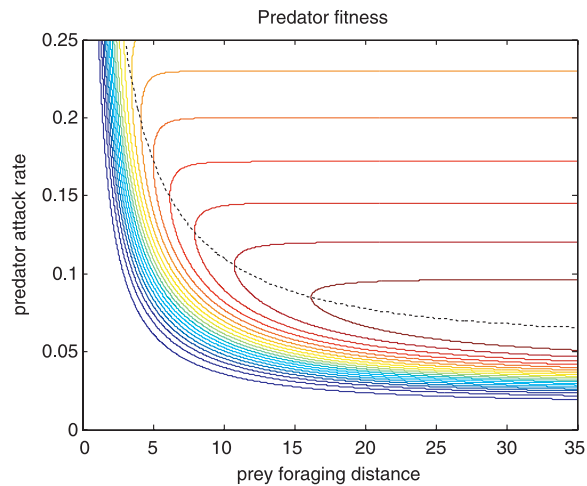


Fig. 3. Prey fitness and optimal response curve. Fitness increases from blue to red.

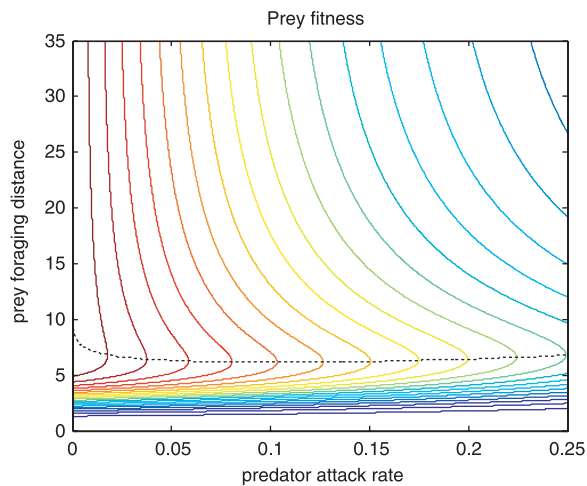


Fig. 4. Predator fitness and optimal response curve. Fitness increases from blue to red.

additional risk of an actual attack. For example, a killer whale might simply cruise past a group of sea lions with its sonar audible and its dorsal fin visible, disrupting foraging but avoiding the risk of injury associated with a direct attack. If the whale did this frequently, so that the sea lions had little time left for foraging, they might be forced out to the more dangerous foraging areas further from the haulout, making it easier for the predator to secure its meals when it needs them.

Figures 6a, b, and c illustrate the effect of additional foraging disruptions caused by killer whales making 0.1, 0.2, or 0.3 of these false attacks per hour. Figures 7a, b, and c show the same prey response curves plotted against the predator's response curve. As the false attack rate increases, the Nash equilibrium moves in the killer whale's favour towards higher foraging distances for the prey and lower true attack rates for the predator. The foraging

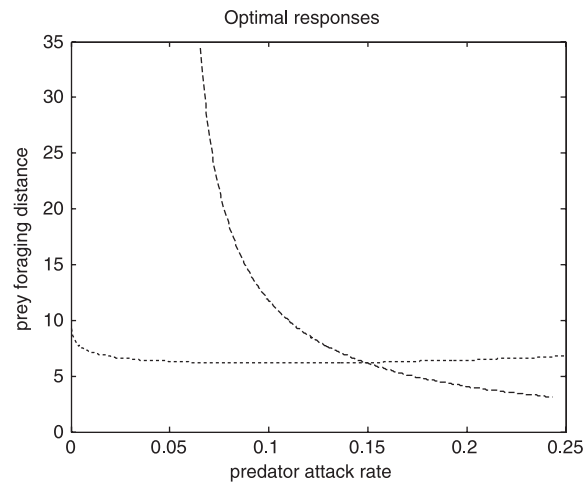


Fig. 5. Curves showing the interaction between the predator response (dashed line) and the prey response (dotted line). Their intersection is a Nash equilibrium.

distance at the equilibrium moves from about 6 km (0 false attacks) to about 15 km (0.3 false attacks per hour), corresponding to approximate capture probabilities of 0.31 and 0.58 respectively.

DISCUSSION

As Figs. 5 and 7 illustrate, an organism's optimal behaviour depends in part on how its adversaries respond to that behaviour. The resulting game may lead to an equilibrium that could not have been predicted without understanding both sides of the interaction.

The game format described here is similar to that used by McNamara *et al.* (1999) to investigate the conflict of interest between two bird parents raising a brood of chicks. This technique is thought to reflect the way in which the system could have approached the intersection over evolutionary time, with entire populations moving towards the equilibrium in successive iterations. Interestingly, if the 'best effort' lines themselves are interpreted as strategies to be used over ecological time, the system proves to be evolutionarily unstable and susceptible to mutant invasion because players oppose each other one at a time – a mutant strategy is effectively never rare.

When there are multiple players on both sides, as in the current predators vs. prey model, mutant strategies are rare (and unlikely to shift equilibria), and the 'best response' lines do work as evolutionarily stable strategies over ecological time. This is an important point, because it implies that a change in the environment could induce a rapid and significant shift in behaviour. For example, if the Steller sea lions in our model were suddenly faced with additional foraging disruptions beyond those caused by their predators, we would predict (based on the analysis illustrated in Fig. 7) an increase both in average foraging distance and in the rate of depredation. Such a scenario might explain part of their recent population crash in terms of foraging disruptions caused by fishing activities near haulouts and rookeries in the first part of the decline (Hennen, 2006; also see Wolf *et al.*, 2006; Wolf and Mangel, submitted).

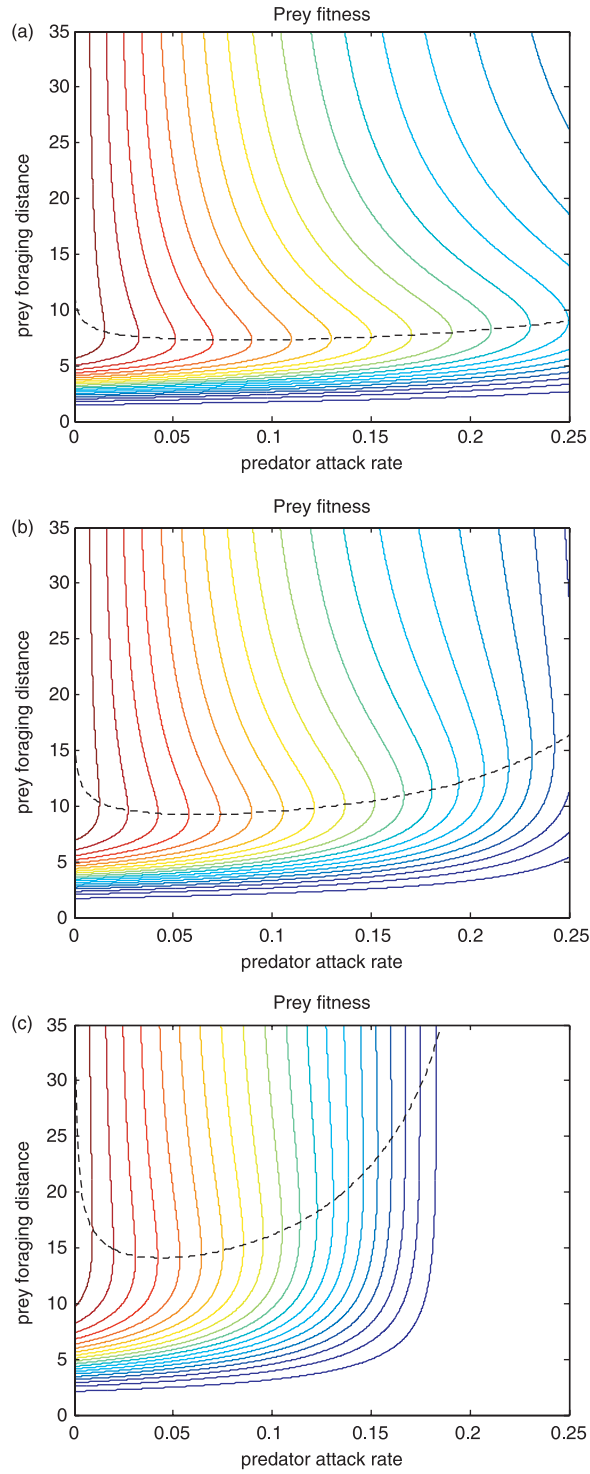


Fig. 6. (a) Prey fitness and response curve with 0.1 additional false attacks per hour. (b) Prey fitness and response curve with 0.2 additional false attacks per hour. (c) Prey fitness and response curve with 0.3 additional false attacks per hour.

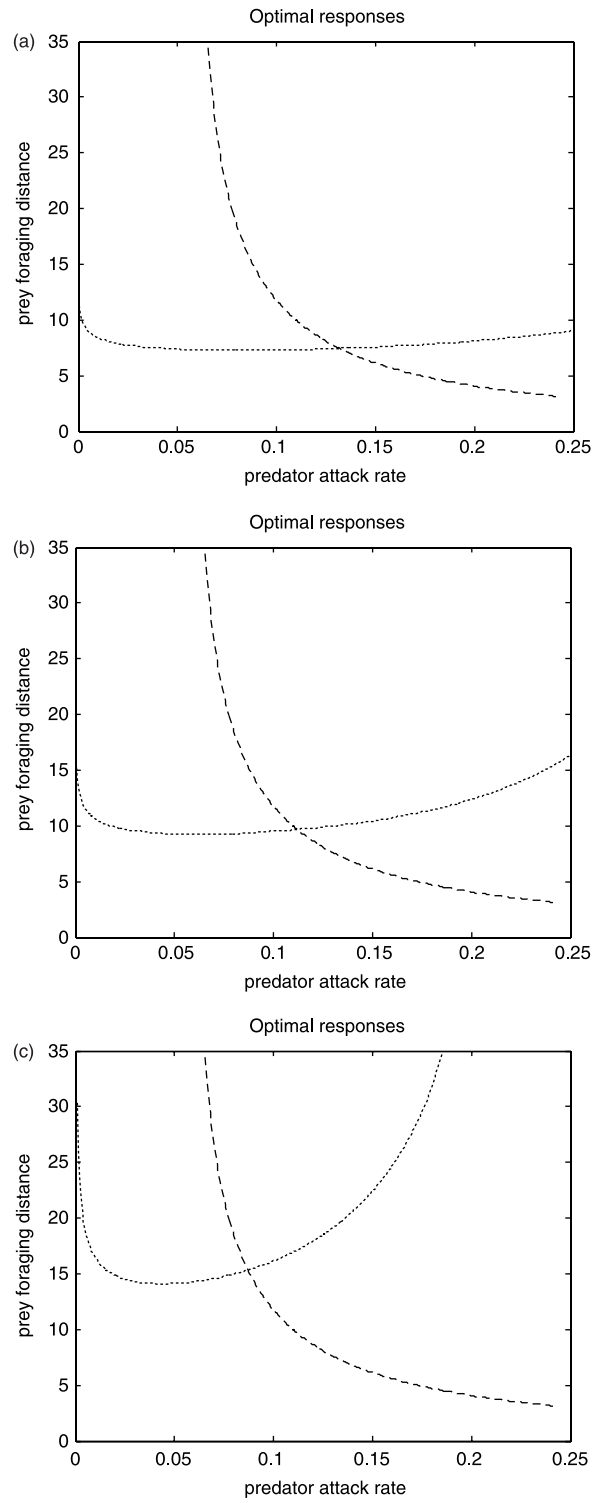


Fig. 7. Predator (dashed)–prey (dotted) interaction curves: (a) 0.1 false attacks per hour, (b) 0.2 false attacks per hour, (c) 0.3 false attacks per hour.

The case for 'false attacks'

The model shows how a predator might exploit the time constraint of its prey and make them easier to catch by disrupting their foraging under false pretences. This novel idea has some basis in observation: Many different types of predators have been observed making casual attack runs with no apparent determination [e.g. avian raptors (Dekker, 1996)], or else 'taunting' or intimidating their quarry (Preisser *et al.*, 2005). In some cases, predator morphology and behaviour may be specifically designed to intimidate. The conspicuous dorsal fin of a killer whale is one example; the distinctive cry of a hawk is another.

One element of the model has already been observed: Foraging animals faced with time limitation do tend to forego anti-predator behaviour (e.g. McNamara and Houston, 1990; Skutelsky, 1996; Yasue *et al.*, 2003; Blumstein and Pelletier, 2005).

The model also predicts that predators will make false attacks in the wild. However, documenting this involves the determination of the predator's intent. It is very difficult to determine whether a predator has made a false attack, or has aborted a serious attack because it lost the element of surprise. A predator behaving optimally might even switch between casual and serious attack modes in mid-attack as the circumstances warrant.

CONCLUSIONS

The 'risk' of predation has two components: the probability of predation mortality, which directly impacts survival, and the set of lost-opportunity costs associated with behaviours reducing the probabilities of encounter, detection, and capture (Lank and Ydenberg, 2003). It is nearly impossible to predict *a priori* the optimal level of anti-predator behaviour (and predation mortality) without knowing the shape of the trade-off function between the two – in other words, without knowing how each component contributes to fitness.

If predators can manipulate prey behaviour by evoking the appearance of an attack without incurring the risk, the situation necessarily becomes more complicated. However, this scenario provides a novel explanation for some elements of predator morphology (conspicuous fins, coloration, calls, etc.) and behaviour (non-serious attacks).

ACKNOWLEDGEMENTS

We thank the Parker and Mangel labs, Akeena Solar, and Katrina Dlugosch for extremely useful comments and support at various stages of the project. N.W. heartily thanks Hanna Kokko, Ian Boyd, Jarl Giske, Rune Rosland, Christian Jorgensen, Oyvind Fiksen, Sigrunn Eliasson, and other members of the Modeling Group in the University of Bergen's Biology Department for their academic encouragement. This work was partially supported by Alaska Fisheries Science Center via contract #AB133F-02-CN-0085 (administered through MRAG Americas), NSF grant DMS 03-10542, the Center for Stock Assessment Research (a partnership between the Santa Cruz Laboratory of the National Marine Fisheries Service and UCSC), and the Lenfest Ocean Program.

REFERENCES

- Alonzo, S.H. and Mangel, M. 2001. Survival strategies and growth of krill: avoiding predators in space and time. *Mar. Ecol. Prog. Ser.*, **209**: 203–217.
- Alonzo, S.H., Switzer, P.V. and Mangel, M. 2003. Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, **84**: 1598–1607.

- Barrett-Lennard, L.G., Ford, J.K.B. and Heise, L.A. 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Anim. Behav.*, **51**: 553–565.
- Blumstein, D.T. and Pelletier, D. 2005. Yellow-bellied marmot hiding time is sensitive to variation in costs. *Can. J. Zool. – Rev. Can. Zool.*, **83**: 363–367.
- Bouskila, A., Robinson, M.E., Roitberg, B.D. and Tenhumberg, B. 1998. Life-history decisions under predation risk: importance of a game perspective. *Evol. Ecol.*, **12**: 701–715.
- Brown, J.S., Laundre, J.W. and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.*, **80**: 385–399.
- Brown, J.S., Kotler, B.P. and Bouskila, A. 2001. Ecology of fear: foraging games between predators and prey with pulsed resources. *Ann. Zool. Fenn.*, **38**: 71–87.
- Clark, C.W. and Mangel, M. 2000. *Dynamic State Models in Ecology: Methods and Applications*. New York: Oxford University Press.
- Dekker, D. 1996. *Hawks: Hunters on the Wing* (Northword Wildlife Series). Minocqua, WI: Northword Press.
- Frid, A., Baker, G.G. and Dill, L.M. 2006. Do resource declines increase predation rates on North Pacific harbor seals? A behavior-based plausibility model. *Mar. Ecol. Prog. Ser.*, **312**: 265–275.
- Guenette, S., Heymans, S.J.J., Christensen, V. and Trites, A.W. 2006. Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. *Can. J. Fish. Aquat. Sci.*, **63**: 2495–2517.
- Hennen, D. 2006. Associations between the Alaska Steller sea lion decline and commercial fisheries. *Ecol. Appl.*, **16**: 704–717.
- Hilborn, R. and Mangel, M. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton, NJ: Princeton University Press.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.*, **91**: 385–398.
- Hugie, D.M. 2003. The waiting game: a ‘battle of waits’ between predator and prey. *Behav. Ecol.*, **14**: 807–817.
- Lank, D.B. and Ydenberg, R.C. 2003. Death and danger at migratory stopovers: problems with ‘predation risk’. *J. Avian Biol.*, **34**: 225–228.
- Lima, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology*, **67**: 377–385.
- Lima, S.L. 2002. Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.*, **17**: 70–75.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.
- Mangel, M. 2006. *The Theoretical Biologist’s Toolbox: Quantitative Methods for Ecology and Evolutionary Biology*. Cambridge: Cambridge University Press.
- Mangel, M. and Clark, C.W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton, NJ: Princeton University Press.
- Mangel, M. and Wolf, N. 2006. Predator diet breadth and prey population dynamics: mechanism and modeling. In *Whales, Whaling and Ocean Ecosystems* (J. Estes, ed.), pp. 277–283. Berkeley, CA: UC Press.
- McNamara, J.M. and Houston, A.I. 1990. The value of fat reserves and the tradeoff between starvation and predation. *Acta Biotheor.*, **38**: 37–61.
- McNamara, J.M., Gasson, C.A. and Houston, A.I. 1999. Incorporating rules for responding into evolutionary games. *Nature*, **401**: 368–371.
- McNamara, J.M., Barta, Z., Houston, A.I. and Race, P. 2005. A theoretical investigation of the effect of predators on foraging behaviour and energy reserves. *Proc. R. Soc. Lond. B*, **272**: 929–934.

- Nash, J. 1950. Equilibrium points in n -person games. *Proc. Natl. Acad. Sci. USA*, **36**: 48–49.
- Polo, V., Lopez, P. and Martin, J. 2005. Balancing the thermal costs and benefits of refuge use to cope with persistent attacks from predators: a model and an experiment with an alpine lizard. *Evol. Ecol. Res.*, **7**: 23–35.
- Preisser, E.L., Bolnick, D.I. and Benard, M.F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**: 501–509.
- Rands, S.A. and Cuthill, I.C. 2001. Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*. *Proc. R. Soc. Lond. B*, **268**: 1783–1790.
- Skutelsky, O. 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. *Anim. Behav.*, **52**: 49–57.
- Willis, J. 2007. Could whales have maintained a high abundance of krill? *Evol. Ecol. Res.*, **9**: 651–662.
- Wolf, N. and Mangel, M. (submitted). Steller sea lions, multiple-hypothesis testing, and the declining-population paradigm: An ecological thriller.
- Wolf, N., Melbourne, J. and Mangel, M. 2006. The method of multiple hypotheses and the decline of Steller sea lions in western Alaska. In *Top Predators in Marine Ecosystems. Their Role in Monitoring and Management* (I. Boyd, S. Wanless and C.J. Camphusen, eds.), pp. 275–293. Cambridge: Cambridge University Press
- Yasue, M., Quinn, J.L. and Cresswell, W. 2003. Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. *Funct. Ecol.*, **17**: 727–736.