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Reversed optimality and predictive ecology: burrowing depth forecasts population change in a bivalve

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Optimality reasoning from behavioural ecology can be used as a tool to infer how animals perceive their environment. Using optimality principles in a 'reversed manner' may enable ecologists to predict changes in population size before such changes actually happen. Here we show that a behavioural anti-predation trait (burrowing depth) of the marine bivalve *Macoma balthica* can be used as an indicator of the change in population size over the year to come. The *per capita* population growth rate between years t and $t+1$ correlated strongly with the proportion of individuals living in the dangerous top 4 cm layer of the sediment in year t: the more individuals in the top layer, the steeper the population decline. This is consistent with the prediction based on optimal foraging theory that animals with poor prospects should accept greater risks of predation. This study is among the first to document fitness forecasting in animals.

Keywords: anti-predation; behavioural indicators; optimal foraging theory; population growth rate

1. INTRODUCTION

In a situation where food and safety are traded off, such as in deciding between feeding in a rich but risky patch or feeding in a poor but safer patch, some individuals may prefer the safer option over the riskier option and *vice versa* (Heithaus *et al.* 2007). To understand such choices, we need to weigh predation risk and food intake on a common scale. Optimality reasoning from behavioural ecology makes this possible (Houston & McNamara 1999). It is not the *risk*, but the *cost* of predation, that can be subtracted as an energetic cost factor from food intake rate (Brown & Kotler 2004; theoretical section, electronic supplementary material). Cost of predation P [J s^{-1}] is risk of predation μ [s^{-1}] multiplied by the future reproductive value F [dimensionless] that is lost when depredated, divided by the marginal fitness value of energy $\partial F/\partial e$ [J^{-1}]:

$$P = \frac{\mu F}{\partial F/\partial e}.$$

Obviously, P increases with μ. Furthermore, individuals that have a high F (i.e. a high expected future fitness) experience a higher cost of predation for a given risk μ than individuals that have a low value of F, where the value of F depends on energy stores, but also varies with other state variables such as health status, age, size (Houston & McNamara 1999). Thus, individuals that have much to lose should be less willing to risk predation than individuals that have little to lose. This life-history principle is coined the 'asset-protection principle' (Clark 1994): F is the asset in need of protection. With an increase in energy stores, the denominator of the equation, $\partial F/\partial e$, declines (and thus P increases) because the relative contribution of energy gain to an animal's F becomes less, the more energy that has been stored (Houston & McNamara 1999). Thus, due to differences in F and in $\partial F/\partial e$, individuals may differ in P at similar values of μ and some may therefore prefer the safer option over the riskier option and *vice versa* (figure S1*a*, theoretical section, electronic supplementary material).

Assuming that natural selection has led to animals being able to accurately assess the costs and benefits of their options and make optimal choices, we can reverse the anti-predation optimization and interpret changes in the options chosen (Kotler *et al.* 2007). Changes in behaviour should reflect changes in food intake rate or changes in one or more of the components of P. Most interestingly, with all else being equal, a change in P could reflect changes in an animal's perception of its future reproductive value F (which it may perceive through, e.g. health changes or changes in its energy stores). If so, we may be able to use (changes in) behaviour to forecast near-future population change, since an individual's perception of F will, to some extent, be a reliable indicator of its actual survival and reproductive chances. Taking this one step further, the perceived F averaged across a sample of individuals may well indicate the population's actual survival and reproductive chances and may thus indicate whether a population is about to increase, decrease or remain stable (Morris & Mukherjee 2007). Note that a change in an individual's survival and/or reproduction does mean a change in its *absolute* fitness, but does not necessarily mean a change in its *relative* fitness (Wilson 2004). If all individuals experience the same change in survival and/or reproduction, then an individual's relative contribution to the gene pool (i.e. relative fitness) will not change. However, we think it is a fair assumption that an individual cannot assess the future reproductive values of other individuals. Under this assumption, an individual not only *perceives* a change in its own survival and/or reproduction as a change in its absolute fitness, but also as a change in its relative fitness.

Here, we present a case for a burrowing bivalve, the Baltic tellin (*Macoma balthica*), whose burrowing depth is typically a reflection of a food-safety trade-off. Burrowing deeper reduces predation risk (Zwarts & Blomert 1992), but also reduces food

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intake (de Goeij & Luttikhuizen 1998). As expected theoretically (Houston & McNamara 1999; theoretical section, electronic supplementary material), *M. balthica* burrows more shallowly when *temporarily* increasing food availability (Edelaar 2000), or when reducing predation danger (Griffiths & Richardson 2006; note that a reduction in predation *danger* reduces predation *risk* in all available options, Lank & Ydenberg 2003). Furthermore, individuals in good condition (experiencing a low $\partial F/\partial e$ and a high F) burrow deeper than those in poor condition (Zwarts *et al.* 1994). We focus on future reproductive value affecting burrowing depth and how it can be used to predict future population changes.

2. MATERIAL AND METHODS

Macoma balthica was sampled annually (1997–2007) during late summer in the intertidal western Dutch Wadden Sea. We visited 2147–2748 stations each year (mean ±s.e.m. = 2618 ± 63). Stations were spatially arranged in a grid with intersections at 250 m intervals (figure 1*a*). At each station, which was reached by foot (low tide; 36% of all stations) or by rubber boat (high tide), 1/56 m^2 of sediment was sampled to a depth of 20 cm. We estimated total density (all samples), but also the proportion of *M. balthica* living in the top 4 cm of the sediment (low-tide stations only), which is the layer that can be accessed by their main predator, the red knot (*Calidris canutus*). Top and bottom were subsequently sieved over a 1 mm mesh. All crustaceans and molluscs that retained on the sieve were counted, collected and stored at −20°C until later analysis. For more details see methods in the electronic supplementary material.

3. RESULTS

From 1997 to 2007, *M. balthica* numbers collapsed by 90 per cent (figure 1*b*; $F_{1,9}=57.0$; $p<0.0001$). Expressing this overall decline as population growth rates between pairs of subsequent years, showed that the population declined during 6 out of 10 years, with the most negative population growth rates in the beginning of the new millennium (figure 1*c*; variation between years: $F_{9,25501}=54.8$; $p<0.0001$). Moreover, an increasing proportion of *M. balthica* (10 mm length class; methods, electronic supplementary material) lived in the risky top layer in the course of our study (figure 1*d*; comparing 1997–2001 with 2002–2006 while weighting for sample size: $F_{1,8}=6.3$; $p<0.05$). Also when including more size classes (8–12 mm), this effect remains ($F_{1,8}=7.9$; $p<0.05$).

4. DISCUSSION

Did the cost of predation (at a given depth) decline over the years, and did this trigger *M. balthica* to burrow more shallowly? Breaking predation cost into its three components, we can ask which cost component has changed: has risk of predation (at a given depth) declined, has the marginal value of energy increased, or has *M. balthica*'s expected future fitness declined?

First, we argue that, at a given depth, risk of predation has not changed. Although *M. balthica*'s main predator, the red knot, has declined in numbers, it has declined at the same rate as its food supply: the density of knots in suitable foraging grounds (i.e. patches where knots could achieve an intake rate more than or equal to 0.3 mg ash-free dry mass s^{-1}) has remained stable over the past decade (Kraan *et al.* in press). With the majority of *M. balthica* living in these dangerous patches (mean ±s.e.m. = 64.3 ± 5.2% from 1997–2005, all size classes; C. Kraan, J. A. van Gils, A. Dekinga & T. Piersma 1997–2005, unpublished data), predation danger (and thus risk at a given depth) must have remained constant. The fact that body mass (expressed as ash-free dry mass), and thus energy stores (Zwarts & Wanink 1993), did not vary between years ($F_{9,633}=1.7$; $p>0.05$ for 10 mm class; $F_{9,2606}=0.7$; $p>0.7$ for 8–12 mm classes), suggests that the marginal value of energy did not change either.

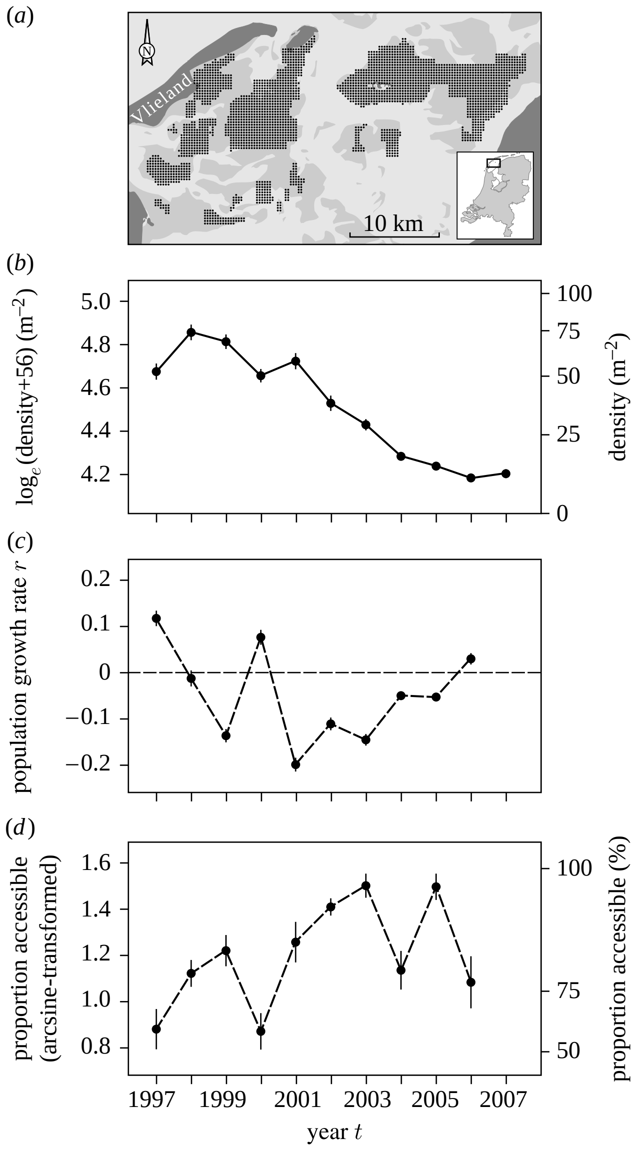

Figure 1. (*a*) The western Dutch Wadden Sea. Dots give sampling stations; shading indicates land (dark grey), intertidal mudflats (intermediate grey) and gullies (light grey). (*b*) *M. balthica* declined by 90 per cent over the last decade (all sizes). Left axis shows transformed values, right axis shows back-transformed values. (*c*) Population growth rate between year *t* and year *t*+1. Horizontal line represents stable population. (*d*) Burrowing depth expressed as the proportion of *M. balthica* in the accessible top layer (10 mm class). Left axis gives arcsine-transformed proportions, right axis gives back-transformed percentages. Dots are means in all graphs; bars are 95% C.I. in (*b*) and s.e.m. in (*c*–*d*).

This leaves us with the third predation-cost factor, future reproductive value, which seems to be able to

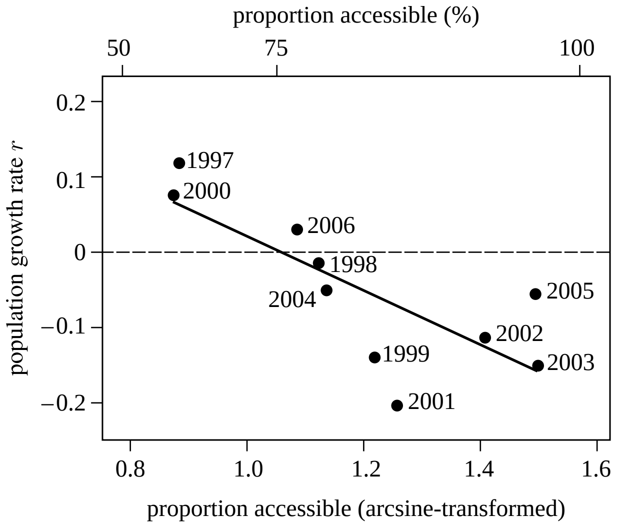

Figure 2. Population growth rate between year *t* and year *t*+1 declined as a function of the proportion of individuals living in the top sediment layer in year *t*. Bottom axis gives arcsine-transformed proportions, top axis gives back-transformed percentages. Line gives GLM regression. Numbers next to dots refer to year *t*.

account for the observed changes in burrowing depth. According to theory, the actual change in population size from year *t* to year *t*+1 should reflect an average *M. balthica*'s perception of its future reproductive value in year *t*. Indeed, we found that the *per capita* population growth rate between year *t* and year *t*+1 correlated strongly with the proportion of individuals living in the dangerous top 4 cm layer in year *t*: the more individuals in the top layer, the steeper the population decline lying ahead (10 mm class: figure 2; GLM; $F_{1,8}=11.3$; $p<0.01$; 8–12 mm classes: $F_{1,8}=7.0$; $p<0.05$).

This decline in future reproductive value could have been due to a long-term decline in *M. balthica*'s food supply. A short-term decline in food availability should make an animal behave less riskily (Houston & McNamara 1999), as confirmed experimentally for *M. balthica* (Edelaar 2000). However, a long-term decline in food availability reduces an animal's perception of its future reproductive value (through reductions in expected survival and fecundity), thereby reducing its cost of predation and thus making it willing to accept greater predation risk in order to enhance its reduced food intake, i.e. burrow more shallowly in the case of *M. balthica* (theoretical section, electronic supplementary material). Indeed, there are indications that diatom abundances have declined over the last decade (Cadée & Hegeman 2002).

If so, then adult mortality rates went up because (i) burrowing more shallowly must have led to greater mortality rates due to predation (at constant predation danger), (ii) reduced food availability probably increased starvation rates (though partly compensated for by a larger feeding radius when burrowed more shallowly (Zwarts *et al.* 1994), which may explain why body mass remained constant over the years). These reduced survival prospects must have brought *M. balthica* even closer to the surface (i.e. the continued reduction in F reinforces a reduction in P), increasing predation rates even further. (This negative spiralling is coined 'the Stalingrad effect' (Brown *et al.* 1997) and is also consistent with theory suggesting that a long-term food reduction may lead to enhanced predation rates, but not necessarily to enhanced starvation rates (Houston & McNamara 1999; figure S1*d*, theoretical section, electronic supplementary material)). Indeed, there is evidence that the population decline is due to reduced adult survival (J. Drent, J. J. Beukema, R. Dekker & K. Essink 1970–2008, unpublished data), in combination with hampered spatfall (correlated with bottom-disturbing fishing and changes in sediment characteristics; Piersma *et al.* 2001) and increased predation on spat (less than 2 mm long) by shrimp, which may be correlated with water temperature changes (Philippart *et al.* 2003).

In an applied context, using an individual's perception of its own prospects as an indicator of population change, one could predict a population crash in the near future, and, if one knows enough about the causes of decline, do something about it (Caro 1998). However, we are most excited about the empirical suggestion that animals are able to reliably assess their own future prospects.

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Brown, J. S. & Kotler, B. P. 2004 Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* **7**, 999–1014. (doi:10.1111/j.1461-0248.2004.00661.x)

Brown, J. S., Kotler, B. P. & Mitchell, W. A. 1997 Competition between birds and mammals: a comparison of giving-up densities between crested larks and gerbils. *Evol. Ecol.* **11**, 757–771. (doi:10.1023/A:1018442503955)

Cadée, G. C. & Hegeman, J. 2002 Phytoplankton in the Marsdiep at the end of the 20th century; 30 years monitoring biomass, primary production, and *Phaeocystis* blooms. *J. Sea Res.* **48**, 97–110. (doi:10.1016/S1385-1101(02)00161-2)

Caro, T. (ed.) 1998 *Behavioral ecology and conservation*. Chicago, IL: University of Chicago Press.

Clark, C. W. 1994 Antipredator behavior and the asset-protection principle. *Behav. Ecol.* **5**, 159–170. (doi:10.1093/beheco/5.2.159)

de Goeij, P. & Luttikhuizen, P. 1998 Deep-burying reduces growth in intertidal bivalves: field and mesocosm experiments with *Macoma balthica*. *J. Exp. Mar. Biol. Ecol.* **228**, 327–337. (doi:10.1016/S0022-0981(98)00062-8)

Edelaar, P. 2000 Phenotypic plasticity of burrowing depth in the bivalve *Macoma balthica*: experimental evidence and general implications. In *The evolutionary biology of the Bivalvia* (eds E. M. Harper, J. D. Taylor & J. A. Crame), pp. 451–458. London, UK: Geological Society.

Griffiths, C. L. & Richardson, C. A. 2006 Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. *J. Exp. Mar. Biol. Ecol.* **331**, 91–98. (doi:10.1016/j.jembe.2005.10.002)

Heithaus, M. R., Frid, A., Wirsing, A. J., Dill, L. M., Fourqurean, J. W., Burkholder, D., Thomson, J. & Bejder, L. 2007 State-dependent risk-taking by green sea turtles mediates top–down effects of tiger shark intimidation in a marine ecosystem. *J. Anim. Ecol.* **76**, 837–844. (doi:10.1111/j.1365-2656.2007.01260.x)

Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour*. Cambridge, UK: Cambridge University Press.

Kotler, B. P., Morris, D. W. & Brown, J. S. (eds) 2007 Behavioral Indicators and Conservation. *Isr. J. Ecol. Evol.* **53**, 229–460.

Kraan, C., van Gils, J. A., Spaans, B., Dekinga, A., Bijleveld, A. I., van Roomen, M., Kleefstra, R. & Piersma, T. In press. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *J. Anim. Ecol.*

Lank, D. B. & Ydenberg, R. C. 2003 Death and danger at migratory stopovers: problems with 'predation risk'. *J. Avian Biol.* **34**, 225–228. (doi:10.1034/j.1600-048X.2003.03250.x)

Morris, D. W. & Mukherjee, S. 2007 Can we measure carrying capacity with foraging behavior? *Ecology* **88**, 597–604. (doi:10.1890/06-0389)

Philippart, C. J. M., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadée, G. C. & Dekker, R. 2003 Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnol. Oceanogr.* **48**, 2171–2185.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J. J., Dekker, R. & Essink, K. 2001 Long-term indirect effects of mechanical cockle dredging on intertidal bivalve stocks in the Wadden Sea. *J. Appl. Ecol.* **38**, 976–990. (doi:10.1046/j.1365-2664.2001.00652.x)

Wilson, D. S. 2004 What is wrong with absolute individual fitness? *Trends Ecol. Evol.* **19**, 245–248. (doi:10.1016/j.tree.2004.02.008)

Zwarts, L. & Blomert, A.-M. 1992 Why knots *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog. Ser.* **83**, 113–128. (doi:10.3354/meps083113)

Zwarts, L. & Wanink, J. H. 1993 How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *J. Sea Res.* **31**, 441–476.

Zwarts, L., Blomert, A.-M., Spaak, P. & de Vries, B. 1994 Feeding radius, burying depth and siphon size of *Macoma balthica* and *Scrobicularia plana*. *J. Exp. Mar. Biol. Ecol.* **183**, 193–212. (doi:10.1016/0022-0981(94)90087-6)