

## *Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology*

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Earlier studies have developed models of carrying capacity to predict the number of animals a certain area can support. These models assume that resources are not renewed after consumption ('standing stock' models), and that the initial number of prey and the rate of prey consumption determine the time a population of foragers can live in an area. Within such areas, foragers give up feeding at a sub-site or patch when intake rates no longer cover energy expenditure. To improve the success rate of the models' predictions, we here change the existing rate-maximising models into fitness-maximising models, and include dynamics in the availability of patches. These new (conceptual) models show that the approaches used so far may over- as well as underestimate carrying capacity. We review empirical studies that have aimed to estimate carrying capacity, and discuss how concepts have been confused. We make explicit suggestions on how to proceed in predicting carrying capacities in future studies.

A forager's intake rate depends on the density of its prey, and this dependency is called the 'functional response'. The most popular form, Holling's disc equation (after Holling 1959), needs just two parameters to calculate intake rates from prey densities: (1) the searching efficiency, and (2) the time it takes to handle one prey item. Traditional distribution models use these expected intake rates to predict whether a patch will be used. According to these models (Piersma et al. 1995), a patch should not be used when it yields an expected intake rate that is below the average intake rate necessary to keep the energy budget balanced over a certain period of time (usually a day). This critical intake rate  $i_c$  is thus a function of the fraction of time available for foraging and of the rate of energy expenditure. The functional response equation can provide the critical prey density  $d_c$  at which  $i_c$  is achieved. In an attempt to make simple predictive models for carrying capacity, Sutherland and Anderson (1993) used this critical prey density to model the number of animal-days an area could support when prey populations are not renewed (Note

that carrying capacity as used here is an energetic rather than a demographic concept, i.e. carrying capacity is expressed as the maximum number of animal-days rather than the maximum number of animals – the latter often being expressed as  $K$  in population models. See also discussion in Goss-Custard et al. 2003.) All prey that are living in densities  $> d_c$  will be consumed, after which all foragers die of starvation or leave the area in search of better alternatives (Fig. 1a). Several field studies have tested the predictions of this model, some with greater success (Vickery et al. 1995) than others (Percival et al. 1998). The good thing about the unsuccessful studies is that they shed light on factors other than prey density that constrain carrying capacity, and that they showed the necessity to include these factors in the model (Percival et al. 1998).

This contribution has three aims. Firstly, we extend existing models on carrying capacity by including (a) fitness costs of foraging (metabolic and predation), and (b) the dynamics of patch availability. Although we acknowledge that all models are simplifications of reality and rough approximations, we feel that the inclusion of costs and constraints will improve the reliability of the predictions made so far (unfortunately at the expense of simplicity). Secondly, we comment on conceptual confusion in the literature: estimates of  $d_c$  are usually not based on energy budget considerations (as explained above), but actually represent giving-up prey densities as observed in the field (GUD, Brown 1988). GUDs are a function of many other trade-offs than the balancing of an energy budget, and can either be higher or lower than  $d_c$ . We hope that alleviating the conceptual confusion with respect to the distinction between  $d_c$  and GUD will improve estimates of carrying capacity. Thirdly, we outline how we think that an ideal predictive study of carrying capacity should proceed.

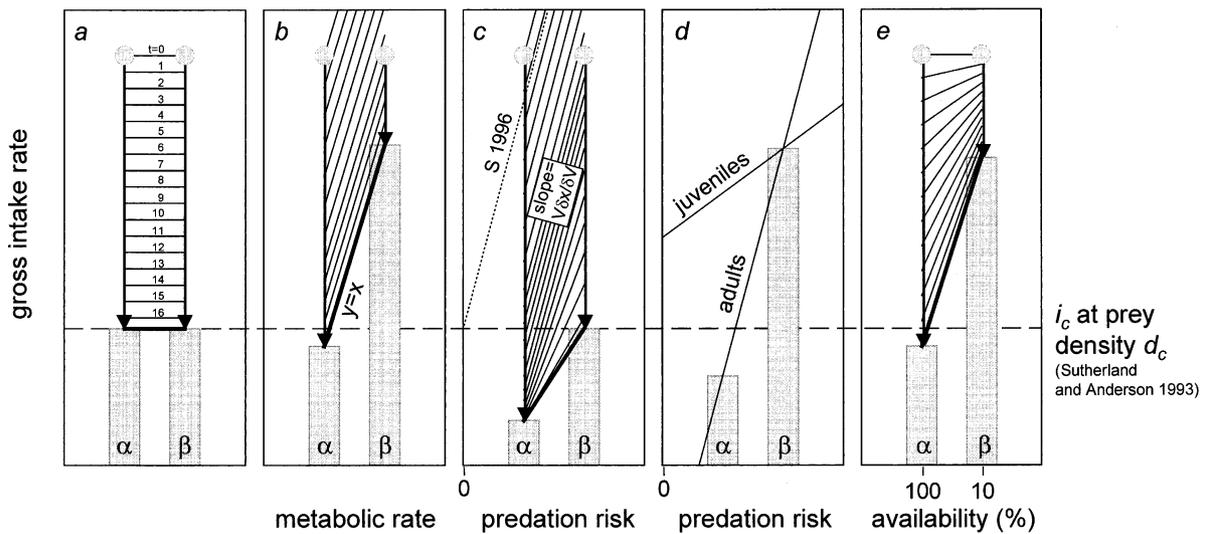


Fig. 1. An area's carrying capacity predicted by the original (a) and by our modified versions (b–e) of the Sutherland and Anderson's (1993)-depletion model. In these examples, the area consists of two patches,  $\alpha$  and  $\beta$ , which initially contain similar prey densities (grey circles). The parameters of the functional response are kept similar across the figures, which enable direct comparisons between predictions of carrying capacity.

(a) In the original model, gross intake rate is the only currency that determines patch use, and therefore both patches are exploited simultaneously from the beginning by frequent switches between them. Due to depletion, prey densities (and thus intake rates) decline over time (arrows). The intervals between the thin lines indicate periods of equal duration (e.g. days or weeks). After somewhat more than 16 time units, the foragers starve, as the intake rate is below the thick line  $i_c$ , the critical level to maintain a positive energy balance (Sutherland and Anderson 1993). Note that the constant distance between the 'time-lines' is explained by the fact that we assumed the foragers to be 'satisficers' that stopped feeding after having obtained their (fixed) daily energy needs.

(b) When patches differ only in the metabolic cost of exploitation it is the *net* intake rate that should be maximised. When plotting gross intake rate on the rate of energy expenditure, the net intake rate increases towards the upper left corner of the graph and lines with a slope of 1 represent lines of equal net intake rate. Thus, the 'cheap' patch  $\alpha$  should be exploited until the net intake rate is down to the level of the 'expensive' patch  $\beta$ , which is after almost seven time units. From then on, both patches will be exploited simultaneously (note that therefore the rate of depletion per patch halves) until the net intake rate in each patch is down to zero (we assume animals can feed for 24 h a day). At that moment (after almost 11 time units), the foragers starve. Since over the entire exploitation period more time has been spent in the cheap patch, the average rate of energy expenditure (and thus  $i_c$ ), is closer to the critical intake rate in the cheap patch than to the one in the expensive patch.

(c) When patches differ only in risk of predation, it is the difference between energy intake rate and predation risk that should be maximised (when expressed on similar scales). When plotting gross intake rate against predation risk, this difference (i.e.  $V_{\text{forage}}$ , the rate of change in reproductive value) increases towards the upper left corner of the graph. Linearly increasing lines with a slope of  $V\delta x/\delta V$  represent lines of equal  $V_{\text{forage}}$ . Thus, patch  $\alpha$  should be exploited until reproductive value changes at a similar rate in patch  $\beta$ , which is after almost seven time units. From then onwards, both patches will be exploited simultaneously until the intake rate in the safe patch is below  $i_c$ . From then on, more and more time should be spent in the dangerous patch  $\beta$  to avoid a negative energy balance. Therefore, daily depletion rates in the dangerous patch get higher and lines of equal  $V_{\text{forage}}$  get shallower. The foragers starve when the intake rate in the dangerous patch has dropped below  $i_c$ , in this case after more than 18 time units. Note that the predation risk model of Sutherland (1996); dashed line indicated by 'S 1996' predicts a much lower carrying capacity.

(d) Individuals that differ in reproductive value experience different costs of predation and therefore may differ in patch choice. If we assume that the adult redshank in the study of Cresswell (1994) have lower reproductive values  $V$  than juveniles, the slope of the lines of equal  $V_{\text{forage}}$  will be steeper in adults than in juveniles (as slope =  $V\delta x/\delta V$ ). Therefore, we can expect situations where adults continuously switch between the safe ( $\alpha$ ) and the risky ( $\beta$ ) patch (for them  $V_{\text{forage}}$  is equal in both patches), but juveniles only feed in the risky patch ( $\beta$ ) (for them  $V_{\text{forage}}$  is largest in  $\beta$ ). This exactly matches the pattern found by Cresswell (1994).

(e) When patches differ only in the daily time they are available, exploitation proceeds quicker in the patch that is most available. In this case patch  $\alpha$  is always available, whereas patch  $\beta$  is available for only 10% of the time. Foraging in patch  $\alpha$  can go on at intake rates below  $i_c$  since foragers can compensate in patch  $\beta$ . Foragers starve when the average intake rate across both patches (weighted for the daily times spent in it) is below  $i_c$ , a situation that in this case is reached after somewhat more than 11 time units.

## Extending traditional models of carrying capacity

### Fitness costs of foraging

In the existing models of carrying capacity, gross energy intake rate is used as the only currency on which patch use decisions are based (Fig. 1a). This approach ignores the various fitness costs of foraging, despite the fact that the presence and importance of such cost factors have been acknowledged a long time ago (Caraco 1979, Gilliam and Fraser 1987). If one takes these additional costs into consideration, an animal should select the patch that yields the highest  $\dot{V}_{\text{forage}}$ , the rate of change in reproductive value. This change is the increase in reproductive value due to net energy gain minus the expected loss in reproductive value due to depredation (Houston and McNamara 1999):

$$\dot{V}_{\text{forage}} = \gamma \frac{\delta V}{\delta x} - MV$$

The first term in this expression is the gain rate in reproductive value, which is the gain rate  $\gamma$  in net energy times the change in reproductive value  $\delta V$  per unit of net energy uptake  $\delta x$ . The second term is the loss rate in reproductive value, which is the risk of predation  $M$  times reproductive value  $V$ . This approach has also been used by Brown (1988), who expresses the rate of change in reproductive value in units of energy turnover:  $\gamma - \frac{MV}{\delta V/\delta x}$ . In this case the second term is called the cost of predation. Below we explore the consequences of the metabolic and predation costs of foraging for traditional carrying capacity models.

#### Metabolic costs

Estimates of  $i_c$ , the critical intake rate to keep the energy budget balanced, are often based on independent measurements of a species' rate of energy expenditure under specified experimental conditions (Piersma et al. 1995). Often, these lab-measurements differ from the actual rate of energy expenditure in the area under consideration. It is obvious that carrying capacity is overestimated when the rate of energy expenditure is underestimated and vice versa. However, over- or underestimates of carrying capacity could still be made if  $i_c$  matches exactly the rate of energy expenditure averaged over the entire exploitation period in the specified area. This could happen when the metabolic costs of foraging differ between patches. For example, Nolet et al. (2001) showed that Bewick's swans (*Cygnus columbianus*) gave up patches at higher food densities when these were energetically more costly to exploit (due to deeper water and more clayey substrate). In the case of diving ducks, *Aythya* spp., van Eerden et al. (1997) also found that the higher costs of diving in deeper water increased GUD.

In such situations, foragers would starve (and thus carrying capacity would be reached) when all patches are harvested down to a level at which the *net* intake rate equals zero in each patch (Note that we assume here that foragers (1) can feed for the entire day, (2) are ideal (they are omniscient with respect to the costs and benefits in each patch), and are free (they pay no time and energy costs when switching between patches)). This implies that the gross intake rate at giving-up, and thus the prey density at giving-up, is proportionally higher in an expensive patch than in a cheap patch. For example, if the area contains just two patches that initially contain similar prey densities, but differ in the metabolic costs of foraging, more time will be spent in the cheaper patch, as it can be harvested down to lower prey densities (Fig. 1b). Thus, the average rate of energy expenditure over the entire exploitation period (and thus  $i_c$ ) is biased towards the rate of energy expenditure in the cheaper patch. Even though more prey are consumed from the 'cheap' patch than expected on the basis of  $i_c$ , much more prey than expected are *not* consumed from the 'expensive' patch (i.e. GUD averaged over the two patches is higher than  $d_c$ ). Thus, the constant  $i_c$ -approach would overestimate carrying capacity of such an area, even though  $i_c$  equals the average rate of energy expenditure over the entire exploitation period. The opposite situation is also possible. If the cheap patch initially contained a lower prey density than the expensive patch, such that less than half of the time would be spent in the cheap patch,  $i_c$  would be biased towards the highest rate of energy expenditure. In the end, average GUD would be lower than  $d_c$  and the carrying capacity would be higher than predicted by a constant  $i_c$ .

#### Predation costs

It is well established that risk of predation influences patch choice decisions of animals (Lima and Dill 1990 for review). When patches differ with respect to gross energy intake rate and risk of predation (but not in metabolic costs), Eq. 1 shows that it is not necessarily the patch with the highest intake or the patch with the lowest risk of predation that should be preferred. Instead, when expressed on the similar scales of reproductive value (Houston and McNamara 1999) or energy gain (Brown 1988), the difference between energy intake rate and predation risk should be maximised. A plot of gross intake rate on risk of predation visualises this difference (Fig. 1c–d). Within such a parameter space,  $\dot{V}_{\text{forage}}$ , the rate of change in reproductive value, goes up towards the upper left corner of the graph (i.e. highest intake at lowest risk) and lines of equal  $\dot{V}_{\text{forage}}$  are linearly increasing. For example, consider two patches that are similar with respect to the metabolic cost of foraging, that initially have similar prey densities, but that differ in the risk of predation (Fig. 1c). A forager will start to feed in the safest patch and deplete

it until  $\dot{V}_{\text{forage}}$  in the safe patch has dropped to the level of  $\dot{V}_{\text{forage}}$  in the dangerous patch. From then on both patches will be exploited such that there is no difference in  $\dot{V}_{\text{forage}}$  between the two patches. Thus, the difference in intake rate is kept constant by frequent switches between the patches and reflects the difference in predation cost (Brown 1988). Towards the end, when the gross intake rate in the safe patch is below  $i_c$ , considerably more time should be spent per day in the dangerous patch, otherwise the forager would starve. In fact, not enough time can be spent in the safe patch to keep the difference in intake rates constant between the patches. This is the reason that the slopes of the lines of equal  $\dot{V}_{\text{forage}}$  decline in the end. This effect can be interpreted as the generalisation that animals close to starvation experience higher marginal values of energy ( $\delta V/\delta x$ ), causing the slope to decline (Houston and McNamara 1999). In spite of this effect, the forager will be able to collect its daily energy requirements as long as it can compensate with an intake rate above  $i_c$  in the dangerous patch. This stops when the intake rate in the dangerous patch has also dropped below  $i_c$ . From that moment onward, the forager starves: carrying capacity of the area has been reached. Traditional carrying capacity models would have predicted both patches to be exploited until  $i_c$  was reached and would thus have underestimated the capacity for fitness-maximising foragers.

Sutherland (1996) has incorporated the effect of predation risk into the Sutherland and Anderson (1993) carrying capacity model (dashed diagonal line in Fig. 1c). Similar to our fitness-based model, GUDs are lower in safe patches than in dangerous patches. However, in his model, carrying capacity approaches zero when prey density in a *completely safe* patch has reached  $d_c$ . In our model, this happens when prey density in the *most dangerous* patch has reached  $d_c$ , which suggests that carrying capacity under the threat of predation might be larger than suggested by Sutherland (1996).

An empirical example of the possible effects of variations in predation costs on patch use decisions is the study by Cresswell (1994). He showed that adult redshank (*Tringa totanus*) preferred to feed in safe habitats at the expense of the rate of energy intake to the extent that these redshanks need to compensate by feeding for half of the day in the risky habitat. They moved to the risky habitat when high tide made the safe habitat inaccessible. The rich but risky habitat was always available but was only exploited when the temporarily available, poor but safe habitat was unavailable. In contrast, juvenile redshank were *always* feeding in the risky but energetically more profitable habitat. As juveniles are likely to have a lower reproductive value  $V$  and thus experience a lower cost of predation, the slopes of lines of equal gain rate  $\dot{V}_{\text{forage}}$  in reproductive value will be shallower, and  $\dot{V}_{\text{forage}}$  will be maximised in

the risky habitat (Fig. 1d). A recent study on starlings (*Sturnus vulgaris*) confirmed the idea that the choice between risky and safe habitat is governed by reproductive value (Olsson et al. 2002).

### Variation in the availability of patches

Apart from ignoring fitness costs in carrying capacity models, ignorance of variation in patch availability may also lead to imprecise estimates of carrying capacity. Although periods of no access to feeding grounds have been built into most models (Piersma et al. 1995, Gill et al. 2001), variation between patches in the length of these periods has never been considered. That foragers respond to such variation is exemplified by the study of Connors et al. (1981), where sanderlings (*Calidris alba*) continuously switch patches when the tide recedes in order to achieve maximum intake rates.

A simple two-patch example shows the dramatic effect of patch availability (Fig. 1e). We assume that there is no difference in the metabolic and predation costs between the patches and that one patch ( $\alpha$ ) is always available and the other ( $\beta$ ) for only 10% of the time. If the patches start off with similar prey densities, the always-available patch  $\alpha$  will be depleted to lower prey densities than the 10%-patch  $\beta$ . From then on, the forager will always aim to feed in the 10%-patch since it yields higher intake rates as it is less depleted. However, if the forager *can* exploit the best patch for only 10% of the time, the remaining 90% of the time it will have to feed in the always-available patch  $\alpha$ . Intake rates in patch  $\alpha$  ( $i_\alpha$ ) can get below  $i_c$  as long as the forager can compensate with high intake rates in patch  $\beta$  ( $i_\beta$ ). The use of both patches comes to an end when the daily *average* intake rate is below  $i_c$ , in this case when  $0.9i_\alpha + 0.1i_\beta < i_c$ . Since more prey above  $d_c$  are *not* consumed from patch  $\beta$  than the extra amount of prey below  $d_c$  that are consumed from patch  $\alpha$ , the final GUD averaged across both patches is higher than  $d_c$ . Thus, the carrying capacity is lower than predicted by the fixed  $d_c$ -approach.

It is also possible to underestimate carrying capacity. The temporally available patch  $\beta$  should be available for more than half of the time (e.g. 90%), and the other one, patch  $\alpha$ , should again be available all the time. Initially, patch  $\beta$  should contain much higher prey densities than patch  $\alpha$ , such that in the end the giving-up density in patch  $\beta$  is still higher than in patch  $\alpha$  (that is, the forager is unable to equalise prey densities across patches). As in the previous case, the forager always prefers to feed in the temporally available patch  $\beta$ , since it yields higher intake rates. The always-available patch  $\alpha$  can now be harvested down to levels *much* below  $i_c$  (since only 10% of the time is spent in there) until  $0.1i_\alpha + 0.9i_\beta < i_c$ . Therefore, in the end, GUD averaged across both patches is lower than  $d_c$ , and thus the

carrying capacity is higher than predicted by the fixed  $d_c$ -approach.

## Discussion

### Do we need to worry about differences between patches within study areas?

We have just claimed that simply considering a fixed prey density  $d_c$  to be the threshold of patch exploitation may lead to imprecise estimates of the carrying capacity of an area. Variation in the (metabolic) costs of living and the availability of patches can lead to either over- or underestimates of carrying capacity. Variation in predation risk leads to underestimates of carrying capacity.

To explore the magnitude of these biases, we looked in more detail at the effect of the cost of predation. This is ecologically the most interesting component of a forager's fitness costs, as it provides information on the forager's state and quality of its environment (Brown 2000), and is often very large (e.g. 8–10 times larger than metabolic cost of foraging in the case of small rodents such as gerbils (*Gerbillus allenbyi*), Brown et al. 1994). As all foragers starve when the intake rate in the most dangerous patch has reached  $i_c$  (Fig. 1c), the underestimation of carrying capacity by Sutherland and Anderson (1993) is due to the *extra* exploitation below  $i_c$  that occurs in safer patches. This is the reason that in our two-patch example we express the magnitude of the underestimation in terms of the final GUD in the *safer* patch at which foragers starve (Fig. 2a). When we divide prey densities by  $d_c$  and predation costs by  $i_c$ , we can interpret the effects in a general way, independent of specific parameters of the study system. How much the safer patch is exploited below  $d_c$  depends on the initial *difference* in predation costs between the two patches, not on the *absolute* values. In addition, it also depends on the initial prey density in the dangerous patch, and not on the initial prey density in the safer patch (given that they both  $\geq d_c$ ). Generally, the safest patch is exploited furthest (as much as to approach emptiness) when the dangerous patch is much more dangerous than the safer patch and contains a high prey density. In such conditions foragers *want to* and *can* spend almost all of their daily time in the safer patch, even when it yields intake rates much below  $i_c$ : since the dangerous patch yields high intake rates, they only need to be there for short periods to compensate.

The effects of this extra use of the safer patch on the number of animal-days can be large. The *relative* amount of extra prey that can be consumed from the safer patch declines with the initial abundance of prey in both patches. Therefore, when patches differ in the associated predation risk, the *relative* underestimation of carrying capacity is largest in areas with low prey

densities (Fig. 2b). Under such conditions, the carrying capacity can be almost twice as large as that predicted using Sutherland and Anderson's approach. This generalisation shows that we *do* need to worry about differences in fitness costs between patches.

### Predictions based on a fixed threshold prey density

In view of these results, the time seems ripe to include these factors in carrying capacity models. Based on some recently published attempts to predict carrying capacity, we will try to describe the way forward.

In the study of Piersma et al. (1995), the distribution of foraging flocks of red knots (*Calidris canutus*) was explained by a fixed  $d_c$ -approach. In their case,  $d_c$  was based on independent experimental measurements of the functional response and of energy requirements in the field. The authors found that 14% of the flocks fed in prey densities below  $d_c$ , and explained this 'deviation' by the suggestion "that red knots are bound to sample unrewarding prey densities". Our two-patch models show that prey densities below  $d_c$  are not necessarily unrewarding for fitness-maximising foragers (this holds for all three scenarios, Fig. 1b–e), and these new models therefore obliterate the need for indirect hypotheses to explain the 'aberrant' 14%.

Studies that consider distribution and depletion over a longer time scale have tested whether a fixed prey density threshold could predict the carrying capacity of an area. Unfortunately, some of these studies (Alonso et al. 1994, Bautista et al. 1995, Smart and Gill 2003) based their prey density threshold on observed GUDs, and then suggested that these threshold densities represent the starvation threshold  $d_c$ . The models presented above clearly show that in a closed system the average GUD deviates systematically from  $d_c$  through variation in fitness costs or patch availability. The studies correctly predicted the observed number of animal-days in an area, but drew the incorrect conclusion that this number represented the carrying capacity of the study area. This mistake stems from the fact that these study areas are never closed systems. When better alternatives exist, (optimal) foragers will leave an area before carrying capacity is reached (Goss-Custard et al. 2002), and therefore observed GUDs may often be higher than the lowest possible GUDs that set carrying capacity.

Another example of what can go wrong in the interpretation of results of empirical work aimed at predicting carrying capacity is the study by Gill et al. (2001). Although they properly used the godwit's (*Limosa limosa*) functional response determined on the basis of field observations in combination with the allometrically predicted field metabolic rate to come to an estimate of  $d_c$  (1000 prey  $m^{-2}$ ), they based their carrying capacity predictions on the lowest observed GUD

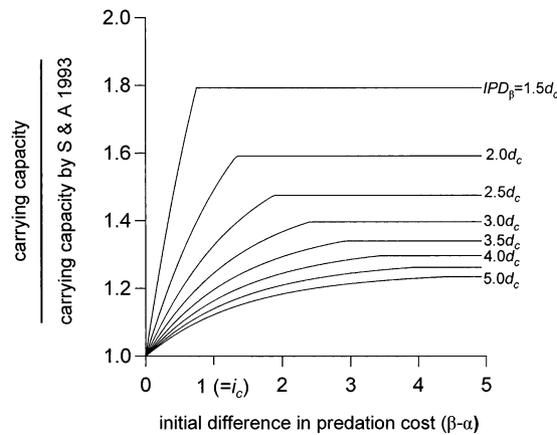
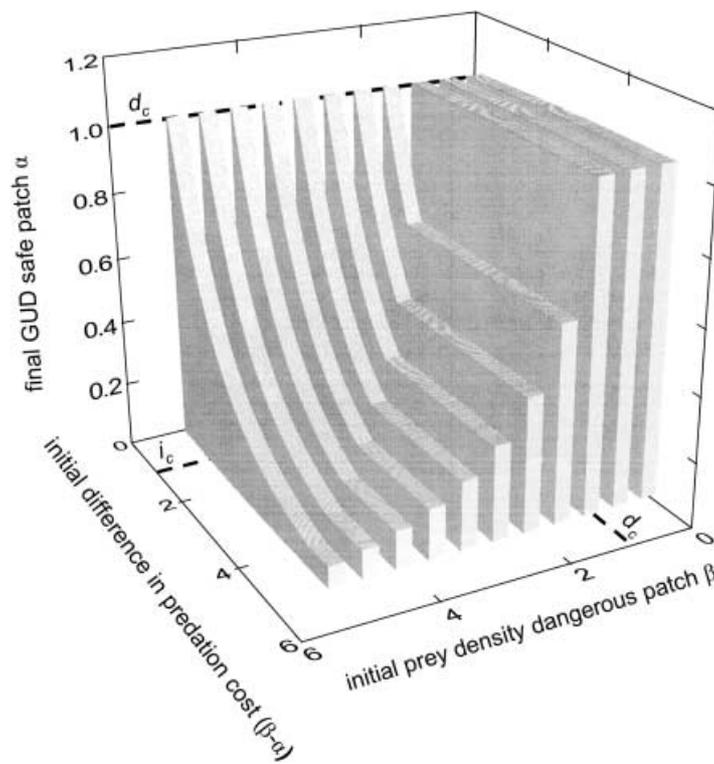


Fig. 2. The quantitative effects of considering the cost of predation on (a) GUD and (b) carrying capacity when two patches differ in risk of predation.

(a) We express the underestimation of carrying capacity by Sutherland and Anderson (1993) as the prey density in the *safer* patch  $\alpha$  at the moment of starvation (the 'final GUD', z-axis in units relative to  $d_c$ ), since prey density in the *dangerous* patch  $\beta$  at the moment of starvation will anyway be at  $d_c$  (Fig. 1c). If we assume that the safer patch initially contains a prey density at or above  $d_c$ , then its final GUD only depends on the initial prey density in the dangerous patch (x-axis, also expressed in units of  $d_c$ ) and the initial difference in predation cost between both patches (y-axis, expressed in units of  $i_c$ ). Only when patches do not differ in their associated cost of predation, or when the dangerous patch starts off at prey densities below  $d_c$ , the safer patch is exploited down to  $d_c$ . For all other starting conditions, the safer patch is emptied more. This is most extreme when foragers *want to* and *can* spend most of their time in the safer patch, even when it yields intake rates much below  $i_c$ . This is the case when feeding in the risky patch is much more dangerous but yields high intake rates. Note that in this case the observed GUD is only a small fraction of  $d_c$  (10–20%); a discrepancy as large as in the study of Gill et al. (2001).

(b) Predicted carrying capacity (of patch  $\alpha$  and  $\beta$  together) relative to the prediction of the Sutherland and Anderson (1993) model, as a function of the initial difference in cost of predation between patches. In this example, prey density in the safer patch initially equals  $d_c$ . When patches do not differ in the cost of predation, Sutherland and Anderson predict similar carrying capacities. We predict higher carrying capacities when this difference increases (again expressed in units of  $i_c$ ), especially when the dangerous patch  $\beta$  contains low initial prey densities (IPD, again expressed in units of  $d_c$ ).

(150 prey m<sup>-2</sup>). In other words, they expected *all* patches to be harvested down to prey densities that were only 15% of  $d_c$ . As our models show, within a habitat, some patches can indeed be exploited well below  $d_c$ , but not all of them! Foragers need to compensate for their net energy losses in patches above  $d_c$  (which are either more dangerous or not always available, Fig. 1c–e). Unfortunately, the authors did not discuss this discrepancy between the calculated  $d_c$  and the observed GUD. With their approach, Gill et al. (2001) demonstrated that the time it took for godwits to deplete prey stocks down to the observed GUD, matched well with the observations on intake rate. This supports the idea that the godwits were the main consumers of the prey stocks, and that the number of godwits at the study sites were counted correctly. But it does not follow, as the authors claimed, that *carrying capacity* is correctly predicted by  $d_c$ , since (1) the authors based their ‘predictions’ on post hoc measurements on GUD and not  $d_c$ , and (2) the capacity of their study area was larger than expected on the basis of a the a priori determined  $d_c$  (i.e.  $GUD < < d_c$ ). Somewhere, apparently outside their study area, the godwits were able to compensate by feeding on prey densities above  $d_c$ . Alternatively, the godwits may have fed on prey types that were not included in the local prey density estimates.

We realise that it is difficult to measure the carrying capacity of an area in the correct way. But we can get quite far if we accept that animals generally do a good job, and that their actual behaviour yields reliable information about their perception of the environment (Wilson 1976, Brown 1988, Olsson and Holmgren 1999, Olsson et al. 1999, 2002). One needs site-independent quantification of the functional response (Piersma et al. 1995) and of the rates of energy expenditure in all patches in the study area (Wiersma and Piersma 1994, Nolet et al. 2001). Once this is established, net intake rates can be predicted from prey density estimates. If foragers feed in patches that differ in predicted net intake rates, patch availability variation may explain part of these differences (the foragers *cannot* always feed in patches that yield maximum net intake rates, Connors et al. 1981). All other unexplained differences in net intake rates may partly be due to the associated differences in predation costs between patches (the foragers do not always *want* to feed in patches that yield maximum net intake rates, Abramsky et al. 2002). Having come to terms with this variation, carrying capacity can then be predicted from the models we outlined. Most importantly, across the patches that are in use, foragers will maintain the observed differences in net intake rates that are due to differences in predation costs (i.e. lines in Fig. 1c remain parallel for almost the entire exploitation period). Depletion will therefore proceed predictably, until the net intake rate in the most hazardous patch is no longer sufficient to com-

pensate for the negative net intakes obtained in safer patches. Future studies are needed on *how* to include other costs factors that influence patch use (physiological damage, risk of infection) to come to even more robust predictions of carrying capacity.

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## References

- Abramsky, Z., Subach, A. and Rosenzweig, M. L. 2002. The cost of apprehensive foraging. – *Ecology* 83: 1330–1340.
- Alonso, J. C., Alonso, J. A. and Bautista, L. M. 1994. Carrying capacity of staging areas and facultative migration extensions in common cranes. – *J. Appl. Ecol.* 31: 212–222.
- Bautista, L. M., Alonso, J. C. and Alonso, J. A. 1995. A field test of ideal free distribution in flock-feeding common cranes. – *J. Anim. Ecol.* 64: 747–757.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk and competition. – *Behav. Ecol. Sociobiol.* 22: 37–48.
- Brown, J. S. 2000. Foraging ecology of animals in response to heterogeneous environments. – In: Hutchings et al. (eds), *The ecological consequences of environmental heterogeneity*. Blackwell Science Ltd, pp. 181–214.
- Brown, J. S., Kotler, B. P. and Valone, T. J. 1994. Foraging under predation: a comparison of energetic and predation costs in rodent communities of the Negev and Sonoran Deserts. – *Austr. J. Zool.* 42: 435–448.
- Caraco, T. 1979. Time budgeting and group size: a theory. – *Ecology* 60: 611–617.
- Connors, P. G., Myers, J. P., Connors, C. S. W. et al. 1981. Interhabitat movements by Sanderlings in relation to foraging profitability and the tidal cycle. – *Auk* 98: 49–64.
- Cresswell, W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? – *J. Anim. Ecol.* 63: 589–600.
- van Eerden, M. R., de Leeuw, J. J., Slager, B. et al. 1997. A field test of the carrying capacity concept in wintering diving ducks: do high foraging costs delimit exploitation of zebra mussels? – In: van Eerden, M. R. (ed.), *Patchwork: patch use, habitat exploitation and carrying capacity for waterbirds in Dutch freshwater wetlands*, Vol. 65. Van Zee tot Land, Lelystad.
- Gill, J. A., Sutherland, W. J. and Norris, K. 2001. Depletion models can predict shorebird distribution at different spatial scales. – *Proc. R. Soc. Lond. B* 268: 369–376.
- Gilliam, J. F. and Fraser, D. F. 1987. Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows. – *Ecology* 68: 1227–1253.
- Goss-Custard, J. D., Stillman, R. A., West, A. D. et al. 2002. Carrying capacity in overwintering migratory birds. – *Biol. Conserv.* 105: 27–41.
- Goss-Custard, J. D., Stillman, R. A., Caldow, R. W. G. et al. 2003. Carrying capacity in overwintering birds: when are spatial models needed? – *J. Appl. Ecol.* 40: 176–187.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. – *Can. Entomol.* 91: 385–398.
- Houston, A. I. and McNamara, J. M. 1999. *Models of adaptive behaviour*. – Cambridge Univ. Press.
- 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.
- Nolet, B. A., Langevoord, O., Bevan, R. M. et al. 2001. Spatial variation in tuber depletion by swans explained differences in net intake rates. – *Ecology* 82: 1655–1667.

- Olsson, O. and Holmgren, N. M. A. 1999. Gaining ecological information about Bayesian foragers through their behaviour. I. Models with predictions. – *Oikos* 87: 251–263.
- Olsson, O., Wiktander, U., Holmgren, N. M. A. et al. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. – *Oikos* 87: 264–276.
- Olsson, O., Brown, J. S. and Smith, H. G. 2002. Long- and short-term state-dependent foraging under predation risk: an indication of habitat quality. – *Anim. Behav.* 63: 981–989.
- Percival, S. M., Sutherland, W. J. and Evans, P. R. 1998. Intertidal habitat loss and wildfowl numbers: applications of a spatial depletion model. – *J. Appl. Ecol.* 35: 57–63.
- Piersma, T., van Gils, J., de Goeij, P. et al. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. – *J. Anim. Ecol.* 64: 493–504.
- Smart, J. and Gill, J. A. 2003. Non-intertidal habitat use by shorebirds: a reflection of inadequate intertidal resources? – *Biol. Conserv.* 111: 359–369.
- Sutherland, W. J. 1996. From individual behaviour to population ecology. – Oxford Univ. Press.
- Sutherland, W. J. and Anderson, C. W. 1993. Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. – *J. Theor. Biol.* 160: 223–230.
- Vickery, J. A., Sutherland, W. J., Watkinson, A. R. et al. 1995. Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L) in relation to food depletion. – *Oecologia* 103: 499–508.
- Wiersma, P. and Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. – *Condor* 96: 257–279.
- Wilson, D. S. 1976. Deducing the energy available in the environment: an application of optimal foraging theory. – *Biotropica* 8: 96–103.