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Skuas at penguin carcass: patch use and state-dependent leaving decisions in a top-predator

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Foraging decisions depend not only on simple maximization of energy intake but also on parallel fitness-relevant activities that change the forager's 'state'. We characterized patch use and patch leaving rules of a top-predatory seabird, the Brown Skua (*Catharacta antarctica lonnbergi*), which during its reproductive period in the Antarctic establishes feeding territories in penguin colonies. In feeding trials, we observed how skuas foraged at penguin carcass patches and analysed patch leaving decisions by incorporating the estimated state of foraging birds and patch availability.

Patches were exploited in a characteristic temporal pattern with exponentially decreasing remaining patch sizes (RPSs) and intake rates. Patch size decreased particularly fast in small compared to large patches and exploitation ended at a mean RPS of 47.6% irrespective of initial size.

We failed to identify a measure which those birds equalized upon patch departure from raw data. However, when accounting for the birds' state, we ascertained remaining patch size and intake rates to have the lowest variance at departure whereas food amount and feeding time remained variable. Statistical correction for territory size only and combined with state had lower effects, but remaining patch size remained the measure with lowest coefficient of variation. Thus, we could clearly reject a fixed-time or fixed-amount strategy for territorial skuas and rather suggest a state-dependent strategy that equalizes remaining patch size. Thus our results provide evidence that under natural conditions, territorial skuas adjust their foraging decision on actual energy requirements, i.e. offspring number and age.

Keywords: offspring provisioning; remaining patch size; intake rate; energy requirements; territoriality; Antarctic

1. INTRODUCTION

According to the marginal-value theorem (MVT), foragers should exploit patches until their intake rate equals the average rate from the environment and thereafter continue foraging in more profitable patches (Charnov 1976). However, quantitative MVT predictions often deviate from empirical tests and suggest that something fundamental is missing (Perry & Pianka 1997; Nonacs 2001). This might be due to the fact that the MVT—though an appealing general concept—is too simple because it assumes patch availability to be known by the forager and more importantly, uses only energy gain as a proxy for fitness and thereby disregards other activities and factors that influence fitness to a major extent. Such activities may include predation avoidance, mate finding or parental care. Thus, their impact on fitness may outweigh the importance of foraging and animals can be expected to incorporate these activities into their foraging decisions. A large body of empirical and theoretical investigations has already shown that animals experiencing predation adjust foraging such that foraging gain is traded-off against predation risk (reviewed in Lima & Dill 1996). However, a more general approach to foraging has been suggested, namely state-dependent foraging (Nonacs 2001). The state of an animal is affected by and will affect foraging decisions and evaluate them with regard to the currency, i.e. fitness determined by survival or provisioning young. Thus, a state-dependent approach considers shifting priorities between life stages, sexes or ages (e.g. Beck *et al.* 2003, Nakashima & Hirose 2003).

Although several theoretical studies have explicitly employed a state-dependent approach to foraging (e.g. Houston & McNamara 1999), empirical tests often lag behind theory (see Clark & Mangel 2000). Foraging under conditions where animals either feed offspring or look for mating opportunities are clearly underrepresented in existing tests of patch use as well as the consideration of individual differences in energy reserves and requirements (Perry & Pianka 1997; Nonacs 2001). Therefore, we investigated foraging behaviour in a top-predatory seabird, the Antarctic Brown Skua (*Catharacta antarctica lonnbergi*), and asked, in particular, whether skuas adjust their foraging behaviour to daily energy demand and general food availability.

Southern hemisphere skuas prey and scavenge in penguin colonies, in which skua pairs may establish feeding territories during breeding (e.g. Trivelpiece *et al.* 1980; Young 1994). Territory owners have nearly

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exclusive access to food within their territory; they successfully defend their territory against intruders and exclude them from foraging. Furthermore, the focal skua population has been extensively studied with regard to the food availability within the feeding territories and, additionally, offspring number and age were known at anytime (Hahn & Peter 2003). Therefore, we can not only characterize the feeding territories of individual skua pairs, but also quantify the energy requirements of their owners throughout the breeding season since they can have one or two young and their food demand also increases during the chick-rearing period.

We observed foraging behaviour of skuas at fresh penguin carcasses killed by skuas in their feeding territories (Hahn & Peter 2003). In particular, we determined general patch exploitation patterns of differently sized penguin carcasses and tested four alternative patch leaving strategies: leave patch after (i) remaining patch size (RPS), or (ii) intake rates fall below a certain threshold; or after having consumed (iii) a fixed amount of food, or after having spent (iv) a fixed time at the patch. For the identification of the patch leaving strategy, we measured how long the birds remained at a patch, how much food they took, calculated intake rates at different exploitation stages and related patch exploitation to the state of the foragers.

2. METHODS

We investigated a population of Brown Skuas at Potter peninsula, King George Island, South Shetlands (62°14′ S, 58°39′ W) between December and February in three consecutive breeding seasons from 1998/1999 to 2000/2001. This population contained 26–32 individually marked breeding pairs, for which offspring number, sex and development were recorded (Hahn & Peter 2003). Approximately one-third of the breeding skuas established feeding territories in a mixed-species penguin colony, where 17 000–20 000 pairs of Adelie (*Pygoscelis adelie*), Gentoo (*Pygoscelis papua*) and Chinstrap penguins (*Pygoscelis antarctica*) bred (Aguirre 1995; Hahn *et al.* 1998). The penguins were not spatially homogeneously distributed but formed approximately 80 subcolonies. On average, a feeding territory contained 421 penguin nests (Hahn & Peter 2003).

For the analysis of patch leaving decisions, we only included territorial breeders because their patch use decisions are less affected by other individuals as they dominate over intruders (Young 1994) and their state can be estimated (see below). In the analyses, we considered pairs as a unit because both sexes engage in offspring provisioning (Pietz 1987).

(a) *General patch exploitation*

We investigated patch exploitation in territories by observing skuas feeding on intact carcasses of 23 Adelie and 6 Gentoo penguin chicks, which had been preyed by the territory owner just before the feeding trial or had starved to death within the last two days. They weighed between 560 and 3445 g, covering the range of patch sizes skuas usually encounter. We classified the carcasses as food patches <1.0 kg ($n=7$, mean±s.d.: 788 ± 150 g), between 1.0 and 2.0 kg ($n=12$, 1413 ± 304 g) and >2.0 kg ($n=10$, 2835 ± 508 g). We conducted the trials throughout the chick-rearing period in intervals of at least 7 days (1999: $n=12$; 2000: $n=10$; 2001: $n=7$), with the earliest and latest trial carried out on 31 December 1998 and 13 February 1998, respectively.

In the course of each trial, we recorded the identity of the foraging bird(s), RPS, exploitation time and intake rates. *Birds' identity*: foragers at a patch were individually identified by leg rings and could either be assigned to a feeding territory (territorial bird) or characterized as intruders, i.e. birds without a feeding territory. RPS (%) was defined as the actual relative to initial carcass mass, whereby actual mass was measured by weighing the carcass on average six times at irregular intervals (Pesola spring balance, ±10 g), i.e. when territory holders adjourned feeding. Patch exploitation time (bird minutes) was defined as the cumulative time individual(s) had been feeding, e.g. two skuas feeding for 1 min results in an exploitation time of 2 bird minutes. Intake rates (g min^{-1}) were calculated from the reduction in carcass mass over exploitation time. Thus, foraging of a single skua resulted in an exact intake rate whereas foraging of more than one individual resulted in an averaged intake rate. We assumed patch use was terminated when either the carcass had been completely used up, i.e. only penguin flippers, tarsi, backbone remained, or the patch had been abandoned for more than 30 min.

(b) *Patch leaving rules of territorial skuas*

We determined the following measures for each patch: (i) total feeding time (min)—the time individuals of a territorial pair fed in a patch, (ii) total food amount (g)—the sum of food they had taken, (iii) intake rate at departure (g min^{-1}) and (iv) RPS at abandonment.

We expected the measure that skuas base their departure decision on to have the lowest coefficient of variation (CV) in all patch classes. We calculated CVs for the four response variables from raw field data and from data fitted by linear mixed effect models. In the latter, we considered daily energy demand per breeding pair (DED_{pair}) and estimated patch availability. We defined state as the DED_{pair} at the time of the feeding trial. DED_{pair} resulted from the requirements of both parents ($\text{DED}_{\text{adults}}$) and their chicks ($\text{DED}_{\text{chicks}}$). $\text{DED}_{\text{adults}}$ was estimated from field metabolic rates of seabirds (Nagy *et al.* 1999) and a food assimilation efficiency of 0.8 (Furness 1978). Given the mean body weight of females (1833 g) and males (1628 g), $\text{DED}_{\text{female}}=2519\ \text{kJ d}^{-1}$ and $\text{DED}_{\text{male}}=2329\ \text{kJ d}^{-1}$. Accordingly, $\text{DED}_{\text{chicks}}$ was calculated as the daily metabolizable energy a chick of a particular age requires divided by a food synthesis efficiency of 0.75 (Ricklefs 1983). As no data for $\text{DED}_{\text{chicks}}$ of skuas exists, we used data from Herring gull (*Larus argentatus*) (Drent *et al.* 1992) and converted these for Brown Skua chicks using a mean fledging mass of 1590 g and an average growth period of 60 days ($\text{DED}_{\text{chick}}=-0.0019x^3+0.0883x^2+2.7635x+10.316$, with $x=$chick age). Number and age of offspring was exactly known for each territorial pair at each feeding trial. In total, DED_{pair} ranged from 4848 kJ (two adults, no chicks) to 7861 kJ (two adults with two chicks aged 42 and 44 days).

We assumed patch availability to be a function of territory size, i.e. larger territories contained more patches. Territory size was estimated yearly by counting the number of penguin nests and ranged from 131 to 2833 penguin pairs per territory (Hahn & Peter 2003).

For the identification of the response variable with the lowest CV and the influence state and territory size have on patch leaving decisions, we calculated the following models

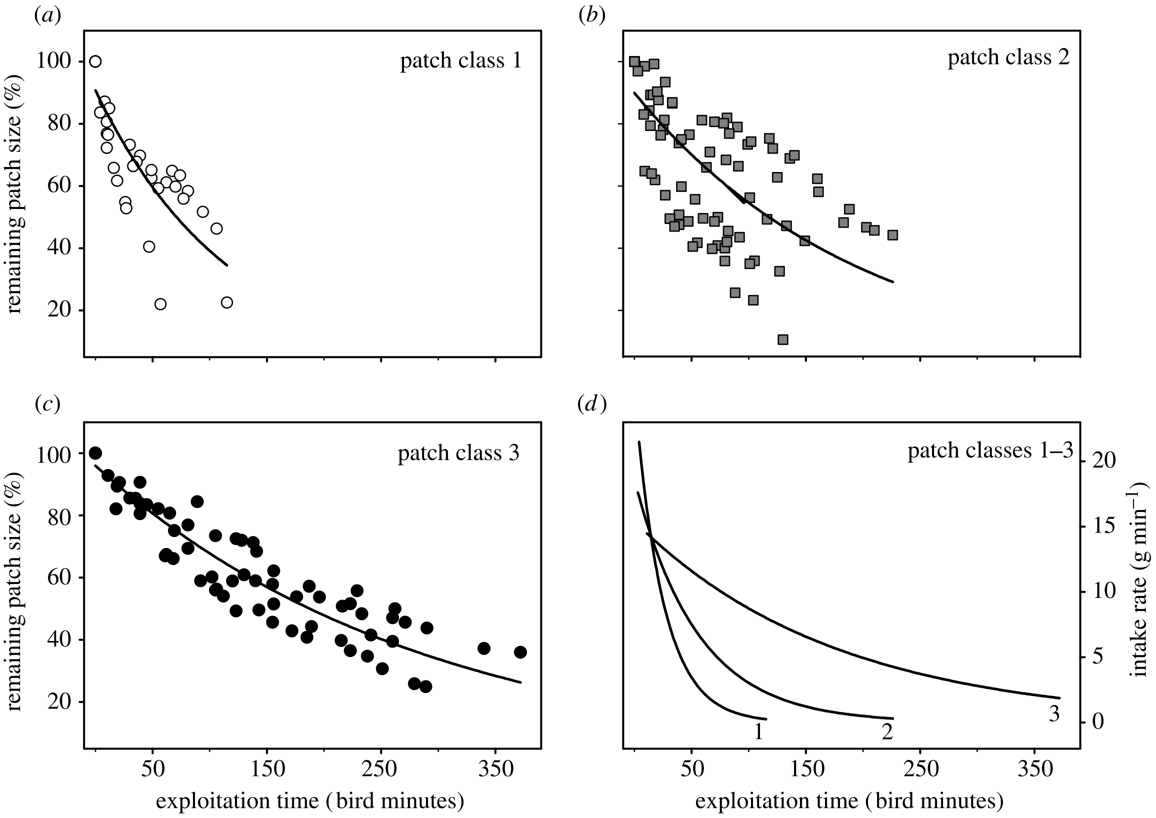

Figure 1. Remaining patch size decreases with exploitation time and the decline is steepest in patch class 1 (*a*), followed by patch class 2 (*b*) and 3 (*c*). Intake rates accordingly diminished with remaining patch size in all classes (*d*) and showed a similar dependence on initial patch size. Data were fitted for $y = a\exp(-bx)$ with x = patch exploitation time (bird minutes) and y = remaining patch size or intake rate (g min^{-1}) for the patch and intake rate model, respectively.

for each response variable (feeding time, food amount, intake rate and RPS).

Model 0: calculation of CVs from raw data. Model 1: calculation of CVs from data which were fitted by a linear mixed effect model (LME) with patch size as fixed factor and DED_{pair} as covariate; data were grouped by Territory ID. Model 2: like model 1, but territory size was the covariate. Model 3: like model 1, but covariate was $\text{DED}_{\text{pair}} \times$ Territory size. All LME models were calculated for each response variable separately. The CVs were calculated from raw data (M0) and fitted values (M1–3) for each variable and patch class. All analyses were conducted with statistical packages R 2.0.0 (LME models) and SPSS 11.0.

3. RESULTS

(a) *Patch exploitation*

Identification of the birds exploiting a carcass showed a typical sequence with territory owners predominantly feeding during the first half of patch use (occurrence 69%), while in the second-half they appeared less often (occurrence 47%) and, consequently, their occurrence at food patches was negatively correlated with exploitation time ($r_S = -0.24$, $p = 0.001$, $n = 2727$). Individuals of other territories, non-territorial breeders and non-breeders foraged only in the absence of territory holders ($r_S = -0.97$, $p = 0.001$, $n = 2727$) and their presence was negatively correlated with RPS ($r_S = -0.22$, $p = 0.008$, $n = 145$) and positively with patch exploitation time ($r_S = 0.22$, $p = 0.001$, $n = 2747$).

Patch exploitation followed the same general pattern in all patch classes: first, patches were rapidly depleted as skuas fed mainly on the easily accessible penguin gut and stomach. Towards the end of patch use, the rate of depletion levelled off when only hardly accessible parts remained, e.g. muscles from the backbone and parts of the skeleton (figure 1). Patch size decreased particularly faster in small compared to large patches (decreasing slopes, *b*, Electronic Appendix; table 1). Exploitation ended at a mean RPS of 47.6% irrespective of the initial size (ANOVA: $F_{2,28} = 0.48$, $p = 0.62$).

Total exploitation time depended on the initial patch mass (linear regression: $r^2 = 0.82$, $p < 0.001$). On average, small patches (patch class 1) were only exploited for 67.0 ± 38.9 bird minutes compared to 259.1 ± 66.1 bird minutes in class 3 patches.

Intake rates decreased exponentially during exploitation and also declined more rapidly in small than in large patches (figure 1, regression statistics in Electronic Appendix table 1). Intake rates were positively correlated with RPS ($r = 0.21$, $p = 0.006$, $n = 168$) and negatively with exploitation time (partial correlation controlled for patch size: $r = -0.40$, $p = 0.001$, d.f. = 165). Maximum intake rate at the beginning of carcass exploitation was 55.5 g min^{-1}. Mean intake rates decreased from 16.9 ± 11.8 g min^{-1} in the first 20 min of exploitation (difference between patch size: $F_{2,22} = 0.10$, $p = 0.90$) to 4.1 ± 3.4 g min^{-1} at the end of feeding trials irrespective of patch class ($F_{2,23} = 1.36$, $p = 0.28$).

(b) *Patch leaving behaviour of territorial skuas*

The time territory-owning skuas fed at a patch depended on initial patch size. In small patches, the birds were feeding only up to 68 min compared to a feeding time

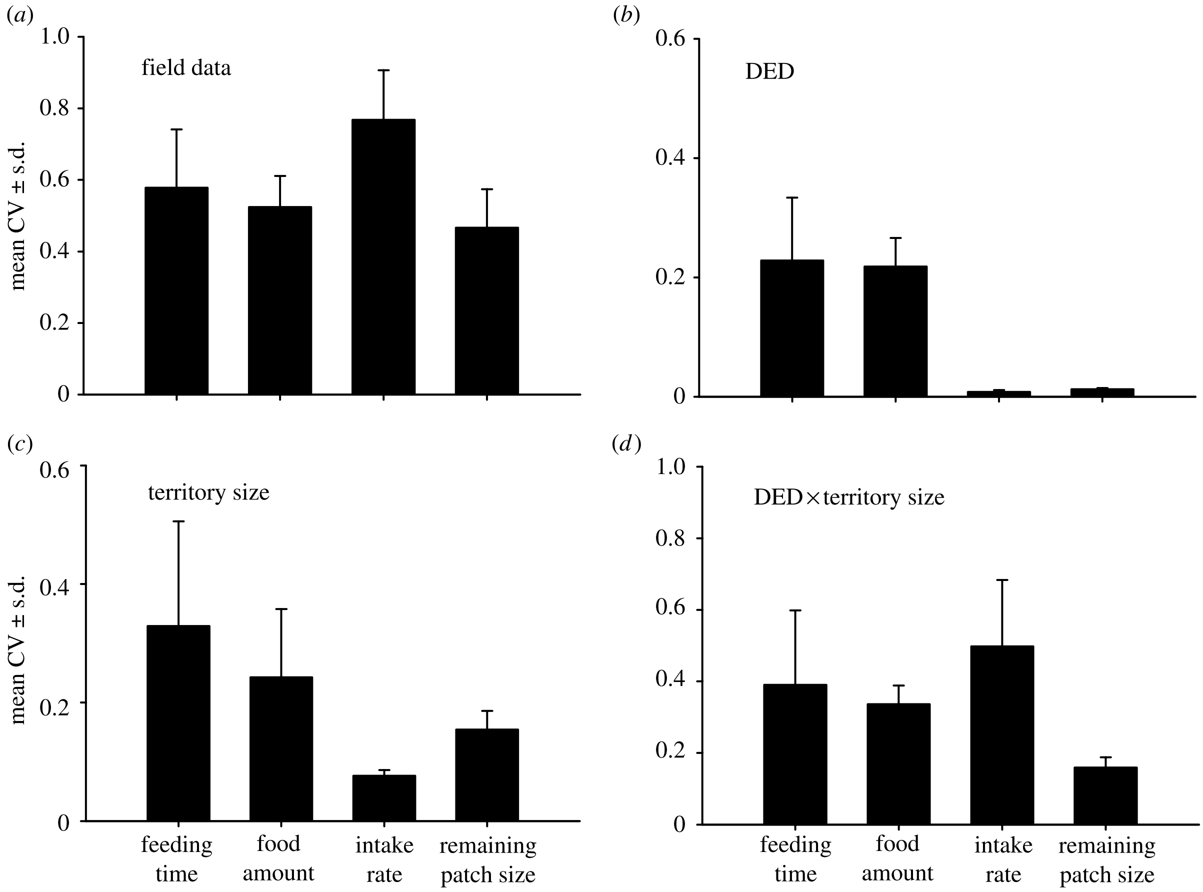

Figure 2. Coefficients of variation (CVs) for the four measures of patch leaving rules: feeding time, food amount, intake rate and remaining patch size. The CVs were calculated from raw field data (*a*; Model 0) and data fitted with a linear mixed effect model that included daily energy demand (*b*; DED, Model 1), territory size (*c*; Model 2) and daily energy demand × territory size as random factors (*d*; Model 3). For calculation details see §2.

of up to 130 min in medium and 157 min in large patches (linear regression: $r^2=0.29$, $p=0.002$, d.f. $=28$ $y=0.032x+25.3$). They received more food in large than in small patches (linear regression: $r^2=0.28$, $p=0.003$, d.f. $=28$; $y=0.190x+173.9$). Asymptotic values of cumulative gain amounted to 330, 588 and 1374 g for patch classes 1–3, corresponding to 42–48% of initial patch weight (see Electronic Appendix; figure 1). However, RPS and intake rates at departure showed no clear dependence on patch size (RPS: $r^2=0.02$, $p=0.46$, d.f. $=28$; intake rate: $r^2=0.01$, $p=0.57$, d.f. $=28$). All LME models yielded the same relations (see Electronic Appendix; table 2).

The CVs from raw field data (Model 0) ranged from 0.47 for RPS to 0.77 for intake rate. They differed neither between the four patch leaving measures nor for different initial patch sizes (ANOVA: factor patch class $F_{2,11}=1.33$, $p=0.33$; factor patch leaving measures $F_{3,11}=3.42$, $p=0.09$ (Model 0, figure 2*a*). However, when including daily energy demand in the analysis (Model 1), CVs differed significantly with the smallest CV for RPS and intake rate (Model 1: ANOVA: factor patch class $F_{2,11}=1.62$, $p=0.28$; factor patch leaving measures $F_{3,11}=15.65$, $p=0.003$, figure 2*b*). The corrected model for territory size (Model 2) gave similar results (ANOVA: factor patch class $F_{2,11}=3.62$, $p=0.09$; factor patch leaving measures $F_{3,11}=5.18$, $p=0.04$, figure 2*c*). When both variables were taken into account (Model 3), RPS at departure again had the smallest CV, but the difference was not statistically significant (ANOVA: factor patch class $F_{2,11}=2.64$, $p=0.15$; factor patch leaving measures $F_{3,11}=4.16$, $p=0.06$, figure 2*d*).

The incorporation of DED in model 1 reduced the variability of the response variables to 1–3% for intake and RPS rate and to 41–43% for food amount and feeding time. Neither the correction for territory size (Model 2) with 11% for intake, 33% for RPS and 50–58% for food and feeding time nor correction for both covariates DED × territory size had such a strong effect (Model 3: 35% for RPS, 65–67% for intake rate, amount of food and feeding time). Thus, given their specific energy requirements territorial skuas equalized RPS of small, medium and large patches.

4. DISCUSSION

In this study, we characterized patch use and identified patch leaving decisions of a top-predatory seabird feeding on terrestrial resources during its reproductive season. The exploitation of penguin chick carcass by skuas showed typical patch use characteristics. The RPS of the carcasses exponentially decreased in the course of exploitation because skuas started foraging typically with taking soft tissues and after longer foraging only hard and tenacious parts remained. Thus, carcasses were non-linearly depleted and consequently, skuas' intake rates decreased with foraging time.

In contrast to other studies, which assumed giving-up densities to be an unambiguous function of quitting intake rates (Brown 1988), we found different intake rates at the same RPS according to initial size. The reasons for these findings might be due to the fact that patches are not uniform throughout, i.e. there are soft and tenacious parts, and, therefore, patch size does not exactly resemble patch density. Moreover, carcasses differ inherently: penguin chicks can have the same mass but different body sizes, i.e. small well-fed chicks versus starving large chicks, such that the proportions of soft parts differ (Myrcha & Kaminski 1982).

Our study suggested a likely patch leaving measure of skuas: they equalized RPS at departure. Thus, these birds employed a similar strategy to what has been referred to as giving-up density strategy. This strategy has been considered optimal when the forager is fully informed about patch density (Garb *et al.* 2000). However, whether an animal can assess patch density depends on its sensory equipment and on the nature and spatial distribution of the food items (Iwasa *et al.* 1981; RodriguezGirones & Vasquez 1997; Vander Wall 1998; Pitt & Ritchie 2002). In contrast, for foragers that cannot assess patch density, abandoning patches after a fixed time pays better (Persons & Uetz 1999; Hayslette & Mirarchi 2002). A third strategy—the fixed amount strategy—is usually expected when foragers are limited in the amount of food they can consume (Brown & Morgan 1995; Svanback & Eklov 2003). Therefore, we conclude that: (1) territorial skuas were able to estimate patch density and (2) they were informed about potential availability of other patches.

However, the result of equalized RPSs appeared in our focal skua population only after accounting for the requirements of another activity—offspring provisioning. To date, most empirical studies investigating foraging under the constraints of other activities focused on predator avoidance (e.g. Brown 1999; Jacob & Brown 2000). Generally, such studies showed that foragers accounted for predator presence in their decisions; however, the evaluation of a site's riskiness again depended on the forager's state. Under low food supply, foragers augmented their use of risky sites (Ylonen *et al.* 2002). Furthermore, differences in food demands during a reproductive period led individuals to bear predation risk sex-specifically (Jormalainen *et al.* 2001; Skals *et al.* 2003).

In a theoretical study, Nonacs (2001) investigated the consequences of state-dependent foraging behaviour in animals that experience simultaneous problems. The results revealed not only a better performance of the state-dependent behaviour but showed that patch use depended on the energy state of the foragers and giving-up densities were not generally equalised across patches. Although we used only a rough estimate for the foragers' state, our results support Nonacs' predictions: individual requirements led to an adjustment of energy intake such that skuas with more or larger young fed more than individuals with less or younger offspring (Model 1, see Electronic Appendix; table 2). Such an adjustment of energy intake according to specific requirements during reproduction or offspring provisioning has been suggested in other studies: lactating bighorn sheep enlarged their bite size (Ruckstuhl et al 2003), Harbour seal (*Phoca vitulina*) females increased foraging effort in the course of the lactating period and lighter females spent more time foraging (Bowen *et al.* 2001).

Our findings showed that territory size had a weaker effect for patch leaving decisions in skuas than actual energy requirement. We would, therefore, conclude that even the smaller territories provided sufficient patches to their owners. However, as territory size varied greatly, we hypothesize that the relation between territory size and patch availability changes within the season and thereby blurs the influence of territory size on patch leaving behaviour. Especially at the end of the Austral summer, we expect territory size to be a stronger predictor of patch availability as by then the number of penguin chicks preyable by skuas diminishes due to predation and chick growth. Future studies should therefore focus on a more elaborate quantification of patch availability.

To our knowledge, this is the first study under natural conditions that incorporates state-dependence in foraging of a large predator and shows that foraging decisions differed according to energy requirements, i.e. offspring number and age. For a more quantitative test of the predictions of state-dependent foraging models, future empirical studies should attempt to explicitly quantify the state of foragers and take it into account when analysing foraging behaviour.

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REFERENCES

Aguirre, C. A. 1995 Distribution and abundance of birds at Potter Peninsula, 25 de Mayo (King George) Island, South Shetland Islands, Antarctica. *Mar. Ornithol.* **23**, 23–31.

Beck, C. A., Bowen, W. D., McMillan, J. I. & Iverson, S. J. 2003 Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Anim. Behav.* **66**, 777–789.

Bowen, W. D., Iverson, S. J., Boness, D. J. & Oftedal, O. T. 2001 Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Funct. Ecol.* **15**, 325–334.

Brown, J. S. 1988 Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47.

Brown, J. S. 1999 Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.* **1**, 49–71.

Brown, J. S. & Morgan, R. A. 1995 Effects of foraging behavior and spatial scale on diet selectivity—a test with fox squirrels. *Oikos* **74**, 122–136.

Charnov, E. L. 1976 Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.

Clark, C. W. & Mangel, M. 2000 *Dynamic state variable models in ecology*. New York: Oxford University Press.

Drent, R. H., Klaassen, M. & Zwaan, B. 1992 Predictive growth budgets in terns and gulls. *Ardea* **80**, 5–17.

Furness, R. W. 1978 Energetic requirements of seabird communities: a bioenergetic model. *J. Anim. Ecol.* **47**, 39–53.

Garb, R. D., Kotler, B. P. & Brown, J. S. 2000 Foraging and community consequences of seed size for coexisting Negev Desert granivores. *Oikos* **88**, 291–300.

Hahn, S. & Peter, H.-U. 2003 Feeding territoriality and the reproductive consequences in Brown Skuas *Catharacta antarctica lonnbergi*. *Polar Biol.* **26**, 552–559.

Hahn, S., Peter, H.-U., Quillfeldt, P. & Reinhardt, K. 1998 The birds of the Potter Peninsula, King George Island, South Shetland Islands, Antarctica, 1965–1998. *Mar. Ornithol.* **26**, 1–6.

Hayslette, S. E. & Mirarchi, R. E. 2002 Foraging-patch use and within-patch diet selectivity in mourning doves, *Zenaida macroura*. *Ecology* **83**, 2637–2641.

Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour: an approach based on state*. Cambridge: Cambridge University Press.

Iwasa, Y. M., Higashi, M. & Yamamura, N. 1981 Prey distribution as a factor determining the choice of optimal foraging strategy. *Am. Nat.* **117**, 710–723.

Jacob, J. & Brown, J. S. 2000 Microhabitat use, giving-up densities and temporal activity as short-and long-term anti-predator behaviors in common voles. *Oikos* **91**, 131–138.

Jormalainen, V., Honkanen, T., Makinen, A., Hemmi, A. & Vesakoski, O. 2001 Why does herbivore sex matter? Sexual differences in utilization of *Fucus vesiculosus* by the isopod *Idotea baltica*. *Oikos* **93**, 77–86.

Lima, S. L. & Dill, L. M. 1996 Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.

Myrcha, A. & Kaminski, P. 1982 Changes in body calorific values during nestling development of penguins of the genus *Pygoscelis*. *Pol. Polar Res.* **3**, 81–88.

Nagy, K. A., Girard, I. A. & Brown, T. K. 1999 Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.* **19**, 247–277.

Nakashima, Y. & Hirose, Y. 2003 Sex differences in foraging behaviour and oviposition site preference in an insect predator, *Orius sauteri*. *Entomol. Exp. Appl.* **106**, 79–86.

Nonacs, P. 2001 State dependent behavior and the marginal value theorem. *Behav. Ecol.* **12**, 71–83.

Perry, G. & Pianka, E. R. 1997 Animal foraging: past, present and future. *Trends Ecol. Evol.* **12**, 360–364.

Persons, M. H. & Uetz, G. W. 1999 Age and sex-based differences in the use of prey sensory cues in wolf spiders (Araneae: Lycosidae). *J. Insect Behav.* **12**, 723–736.

Pietz, P. J. 1987 Feeding and nesting ecology of sympatric South Polar and Brown Skuas. *Auk* **104**, 617–627.

Pitt, W. C. & Ritchie, M. E. 2002 Influence of prey distribution on the functional response of lizards. *Oikos* **96**, 157–163.

Ricklefs, R. E. 1983 Avian postnatal development. In *Avian biology* (ed. D. S. Farner, J. R. King & K. C. Parkes), vol. 7, pp. 1–83. New York: Academic Press.

RodriguezGirones, M. A. & Vasquez, R. A. 1997 Density dependent patch exploitation and acquisition of environmental information. *Theor. Popul. Biol.* **52**, 32–42.

Ruckstuhl, K. E., Festa-Bianchet, M. & Jorgenson, J. T. 2003 Bite rates in Rocky Mountain bighorn sheep (*Ovis canadensis*): effects of season, age, sex and reproductive status. *Behav. Ecol. Sociobiol.* **54**, 167–173.

Skals, N., Plepys, D. & Lofstedt, C. 2003 Foraging and mate-finding in the silver Y moth, *Autographa gamma* (Lepidoptera: Noctuidae) under the risk of predation. *Oikos* **102**, 351–357.

Svanback, R. & Eklov, P. 2003 Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos* **102**, 273–284.

Trivelpiece, W. Z., Butler, R. G. & Volkman, N. J. 1980 Feeding territories of Brown Skuas (*Catharacta lonnbergi*). *Auk* **97**, 669–676.

Vander Wall, S. B. 1998 Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. *Ecology* **79**, 233–241.

Ylonen, H., Jacob, J., Davies, M. J. & Singleton, G. R. 2002 Predation risk and habitat selection of Australian house mice, *Mus domesticus*, during an incipient plague: desperate behaviour due to food depletion. *Oikos* **99**, 284–289.

Young, E. C. 1994 *Skua and penguin, predator and prey*. Cambridge: Cambridge University Press.

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