

Does Prey Capture Induce Area-Restricted Search? A Fine-Scale Study Using GPS in a Marine Predator, the Wandering Albatross

Henri Weimerskirch,^{*} David Pinaud,[†] Frédéric Pawlowski,[‡] and Charles-André Bost[§]

Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France

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ABSTRACT: In a patchy environment, predators are expected to increase turning rate and start an area-restricted search (ARS) when prey have been encountered, but few empirical data exist for large predators. By using GPS loggers with devices measuring prey capture, we studied how a marine predator adjusts foraging movements at various scales in relation to prey capture. Wandering albatrosses use two tactics, sit and wait and foraging in flight, the former tactic being three times less efficient than the latter. During flight foraging, birds caught large isolated prey and used ARS at scales varying from 5 to 90 km, with large-scale ARS being used only by young animals. Birds did not show strong responses to prey capture at a large scale, few ARS events occurred after prey capture, and birds did not have high rates of prey capture in ARS. Only at small scales did birds increase sinuosity after prey captures for a limited time period, and this occurred only after they had caught a large prey item within an ARS zone. When this species searches over a large scale, the most effective search rule was to follow a nearly straight path. ARS may be used to restrict search to a particular environment where prey capture is more predictable and profitable.

Keywords: foraging, first-passage time, area-restricted search, sinuosity, age.

Predators should make optimal decisions about where and how to forage to maximize both their efficiency and, ultimately, their fitness (Stephens and Krebs 1986). In doing

so, they should choose the habitat that yields the highest reward, searching more thoroughly for prey in some areas than in others, as a response to spatial prey density (Curio 1976). Several predictions about how predators should adjust their movements in response to prey capture have been made. For example, it has been predicted that predators should increase turning rate once prey have been encountered or in response to environmental cues and that search behavior should be scale dependent (Fauchald 1999). However, very few empirical data are available to test these predictions, especially in the marine environment. In a continuous patchy environment, it is expected that predators should increase search effort after detecting a prey item because of the high probability of encountering other prey items nearby (a behavior generally referred to as area-restricted search [ARS]; Kareiva and Odell 1987), before continuing a wider-range exploration and moving from one spatially delimited resource patch to another. It is thus predicted that animals engaging in ARS should follow a sinuous search path (Bover and Benhamou 1988) immediately after capturing prey items (Kareiva and Odell 1987). Empirical evidence supporting this prediction has generally come from detailed studies of insects foraging over small-scale habitats (e.g., Kareiva 1990; Wiens et al. 1997), whereas detailed large-scale foraging studies are extremely rare (Turchin 1998). More often, theoretical, experimental, and field observations have concentrated on the problem of efficient patch use from the perspective of patch departure rules, wherein predators are predicted to maximize their mean rate of energy intake by leaving patches when the rate of intake from the patch collapses to the overall mean rate of intake from the environment (marginal value theorem; Charnov 1976). It is therefore surprising that the question of whether ARS is induced by prey capture has received relatively little attention (Walsh 1996), especially for vertebrates. Understanding the conditions that lead predators to start ARS is even more complicated because decisions to modify behavior after prey capture are likely to depend on many parameters, such as

^{*} Corresponding author; e-mail: henriw@cebc.cnrs.fr.

[†] E-mail: puffin@cebc.cnrs.fr.

[‡] E-mail: pawlowski@cebc.cnrs.fr.

[§] E-mail: bost@cebc.cnrs.fr.

the presence of other predators or congeners, the state of the forager, the cost of catching the prey, the quality of the prey patch, or predation risks (Walsh 1996; Nonacs 2001). In addition, because predators are likely to forage in a hierarchical patch system, in which patches at small scales are nested in patches at larger scales (Kotliar and Wiens 1990), they are expected to have a scale-dependent search strategy whereby they modify their search pattern according to recent foraging success (Fauchald 1999). Predators would therefore be expected to employ a scale-dependent foraging strategy as an answer to hierarchical aggregation of prey.

In the marine habitat, where it is rarely possible to make direct observations of prey capture, studies on foraging decisions in relation to prey capture are almost nonexistent. Only a few studies have been able to measure prey capture along foraging paths (Weimerskirch et al. 1994, 2005; Sims and Quayle 1998; Austin et al. 2006) but only with low accuracy or over short periods. Prey encounter rate is likely to play a major role for these predators as they adjust their searching movements at small spatial scales, especially at high prey density (i.e., in a dense patch), whereas past experiences, combined with abilities to return to a particular marine area, are expected to act mainly in large-scale movements at a scale where prey distribution is more predictable (Hunt et al. 1999). Studying movements at smaller scales in relation to prey capture is therefore crucial to better understanding scale-dependent adjustments of such long-ranging predators.

By using a high-precision locating system (GPS sampling every 10 s; Weimerskirch et al. 2002) together with a logger measuring timing of prey ingestion and prey size (Wilson et al. 1995), we have been able to more accurately study foraging decisions in relation to prey capture in a central-place foraging marine predator. Specifically, we have recorded the foraging behavior and foraging success of wandering albatrosses (*Diomedea exulans*) of known age during a period of high energy demand for a pelagic seabird, the brooding period (Ricklefs 1983). Here, our goal was to determine whether and under what conditions a marine predator would modify its behavior after a prey capture. By using this method, it was also possible to associate foraging decisions with habitat use (whether birds were foraging over oceanic or neritic waters) and mode of foraging (sit and wait vs. active foraging; Pianka 1966). Because in natural systems predators respond to a range of environmental features at different spatial scales, it is necessary to quantify when and at which scale they concentrate their search efforts along a path. Therefore, we used recently developed first-passage time (FPT) analysis (Fauchald and Tveraa 2003) to determine when ARS occurred along the foraging path.

Methods

Species and Field Study

Wandering albatrosses are large (8–12 kg) seabirds that breed on sub-Antarctic islands. During the breeding season, they are able to forage thousands of kilometers from the colonies by using gliding flight that extensively reduces flight costs (Weimerskirch et al. 2000). They feed mainly on a wide variety of squids that are captured or found dead at the sea surface (Cherel and Weimerskirch 1999). They forage over two bathymetric habitats, the shelf areas, or neritic waters (shallower than $-2,000$ m), and oceanic waters (deeper than $-2,000$ m).

The study was carried out on Possession Island (46°S, 51°E), Crozet Islands, southwestern Indian Ocean (fig. 1), during the brooding periods in 2002–2005. The age, sex, and previous breeding experience of individuals were known from our long-term database (Weimerskirch and Jouventin 1987). A total of 45 individuals of both sexes that were brooding chicks from 10 to 20 days old were fitted simultaneously with a GPS tag and a stomach temperature transmitter and associated receiver-recorders, but because of various electronic problems, data from both loggers were usable for only 27 individuals (14 males and 13 females). We classified individuals into younger (6–13 years, $n = 9$) and older birds (16–40 years, $n = 18$). Birds were caught by hand as they were about to leave the colony to forage, after having been relieved from brooding duties by their partner. After being weighed and instrumented, they were released and generally took off within minutes. The GPS tag (New Behaviour, Zurich; 45 g; see Steiner et al. 2000) were programmed to one location (± 5 m) every 10 s (Weimerskirch et al. 2002). Temperature recorders were used to estimate the timing of prey ingestion and the mass of prey swallowed (for estimation of mass of prey, see Wilson et al. 1995). The birds were induced to swallow a 20-g stomach temperature pill that transmits the temperature of the stomach to a recorder (Wildlife Computer, Redmond, WA; 25 g) that receives and stores every 15 s the information sent by the pill. The GPS tag and the recorder were attached with white TESA tape on the back feathers. This procedure has been used for 12 years on albatrosses (Weimerskirch et al. 1994) and can be done quickly to minimize handling stress. This procedure also allowed us to recover loggers without damaging feathers (Wilson et al. 1997). The total mass of the equipment was 90 g (0.7%–1.2% of body mass), which is well below the generally accepted 3%–5% threshold for adverse behavioral effects (Croll et al. 1992; Phillips et al. 2003).

Birds were recaptured after they had returned to their nest, equipment was removed, and the bird was weighed. We had no chick desertion during the instrumentation and removal of loggers, and no effects were observed on

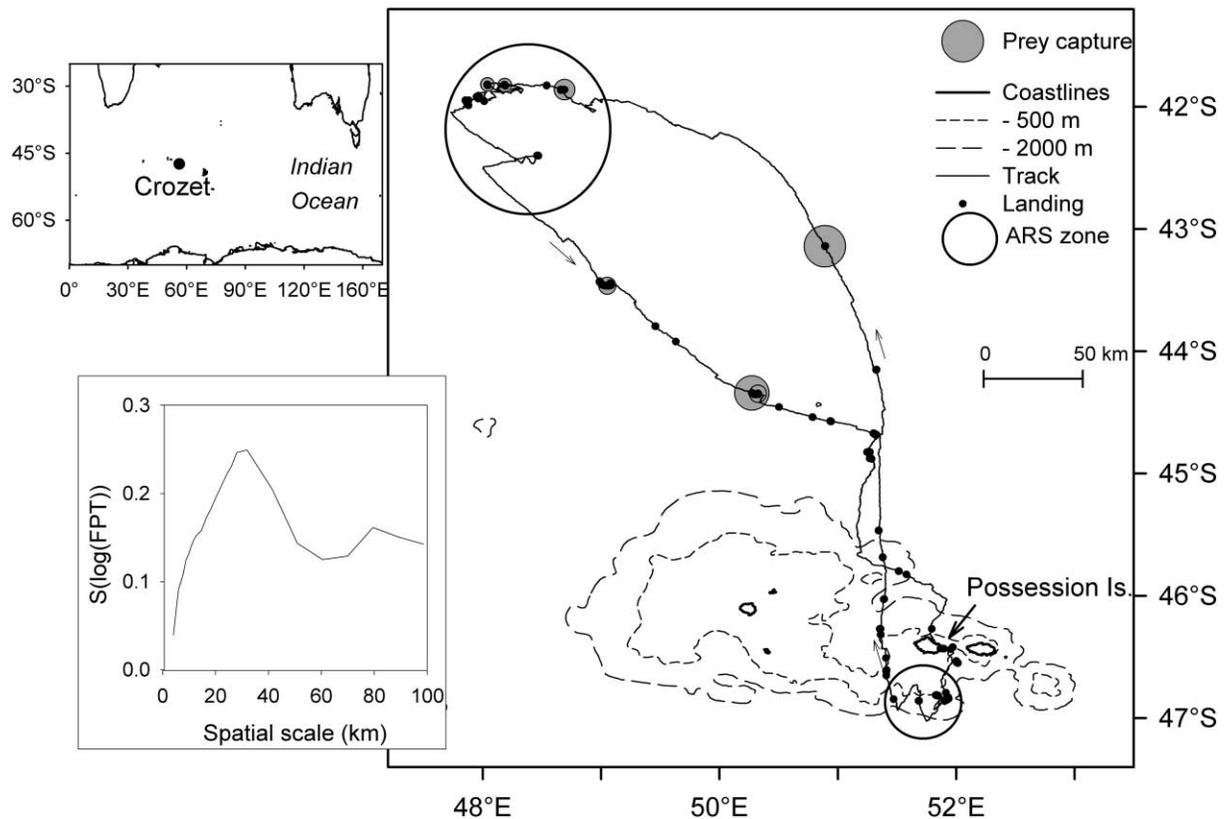


Figure 1: Movement of foraging wandering albatross F from the Crozet Islands tracked by GPS and fitted with a stomach sensor. Prey capture events are indicated by gray circles (sizes are proportional to the mass of the prey). Large open circles indicate zones of area-restricted search (ARS) and are proportional to the scale of the ARS zone. Upper inset shows southern Indian Ocean with the study area. Lower inset shows plot of variance in $\log(\text{first-passage time})$ in function of spatial scale for individual F, showing two peaks of variance, indicating ARS at the corresponding scales of 30 and 80 km.

either adult survival or breeding success. The presence of the pill was checked with a metal detector just after equipment fitting and on return to the nest. Wandering albatrosses regularly regurgitate pellets made of hard parts of prey, such as squid beaks, and consequently, they regularly regurgitate pills. Thus, to avoid additional stress of stomach lavaging, stomach temperature pills were left in situ for birds to regurgitate on their own. Fifty-four percent of the pills were missing from the stomachs of the birds when they returned to the nest after a first foraging trip, and our previous studies (Weimerskirch et al. 1994, 2005) indicate that loggers are regurgitated within 1 month after being inserted. The durations of trips in this study were similar to those of uninstrumented birds studied during other years (2.8 ± 0.9 vs. 2.9 ± 0.7 days; $F = 0.12$, $df = 1, 98$, $P = .921$; Weimerskirch and Lys 2000), suggesting that there was little effect of the stomach temperature logger or GPS tag on performance (see also Weimerskirch 1995).

Data Processing

GPS locations were used to study movement pattern and sinuosity of foraging tracks, as well as time spent on the water. Birds were considered to be sitting on the water when movement speed between three consecutive locations (i.e., 30 s) was $<10 \text{ km h}^{-1}$, because birds cannot stay aloft at such speed (see Weimerskirch et al. 2002). The stomach temperature data were analyzed using Software MT (Jensen Software, Loehe, Germany), which detects the precise timing of feeding events from the precipitous drop of the stomach temperature and gives an estimate of the mass of prey from the integral of the record of the precipitous drop followed by an exponential rise in temperature (PDER; see Wilson et al. 1995). Water ingestion (or prey composed mainly of fluid, such as jellyfish) was separated from prey ingestion based on the shape of PDER, following Catry et al. (2004), and all water ingestion events (14% of captures) were excluded from the

analysis. For some analyses, prey ingestions were separated into small prey (mass <500 g) and large prey (mass >500 g). Locational data and feeding events were merged with environmental data (i.e., bathymetry). Because birds may have regurgitated the stomach pill before they returned to the colony (but the recorded information is still retained on the receiver-recorder on the back), some temperature recordings were incomplete. For these tracks, the analysis was performed only on the part of the track during which the bird was carrying the pill. Prey were considered as being caught in a same patch when (a) they were caught such that there was no take-off movement between two prey captures or (b) they were caught within a distance of <1 km of each other (see Weimerskirch et al. 2005).

Data Analysis

To estimate zones of ARS, we applied FPT analysis, following Fauchald and Tveraa (2003) and using software R 2.1.1 (R Development Core Team 2005). FPT is based on the calculation of the time required for an animal to cross a circle with a given radius, as a scale-dependent measure of search effort. This analysis allows the identification of the spatial scales at which an animal concentrates its search effort (increases of sinuosity and/or decreases in movement speed). A preliminary application of FPT analysis on GPS tracks showed that very small-scale ARS zones (<100-m diameter), which corresponded to when the bird was sitting on the water, dramatically inflated the variance in FPT and reduced the ability to detect larger-scale ARS zones (>100-m diameter). To remove this problem, we considered bouts on the water as flying bouts with a constant speed of 30 km h⁻¹ (minimum sustained flight) and interpolated locations to obtain a distance interval of 1 km for FPT analysis (for validation of this method, see Pinaud 2007). FPT was calculated every 1 km for a radius r from 1 to 100 km. The plot representing variance in log(FPT) as a function of r allowed us to identify the ARS scales by peaks in the variance (see fig. 1). In this calculation, FPT was log transformed to make the variance independent of the magnitude of the mean FPT (see Fauchald and Tveraa 2003). By considering the plot of FPT values where a peak of variance occurred as a function of time elapsed since departure from the colony (see fig. 3 in Fauchald and Tveraa 2003), it is possible to locate where the bird enters an ARS zone. FPT values were smoothed following the LOWESS algorithm of Cleveland (1981), with $0.005 < f < 0.03$. An FPT value threshold was determined according to its multimodal distribution: ARS zones corresponded to the mode of higher FPT values (Pinaud 2007).

In addition to the FPT analysis, we used a simple measure of sinuosity (Benhamou 2004) to investigate whether

birds tended to modify their small-scale movements (<1 km) after a prey capture. We measured sinuosity of the flight track, as measured by the ratio of the straight-line distance between the initial and the final position relative to the actual path (Weimerskirch et al. 2002) 2, 10, and 20 min before and after each prey capture event. Because sinuosity can be affected by local wind conditions (Weimerskirch et al. 2002), to test the hypothesis that birds were modifying their sinuosity in response to prey capture, we measured the ratio of changes in sinuosity before and after prey capture.

To analyze the effects of various factors (sex, age class, year) on dependent variables such as prey mass, proportional change in sinuosity, or distance between prey, we first checked for normality. If the distribution was significantly different from normality, we log transformed the data and checked again for normality. Because several prey captures occurred during a foraging trip, data for prey mass and time between prey captures were analyzed using mixed-effects ANOVAs. Mass of prey, distance between prey, and foraging success were the dependent variables; the individual was a random factor; and sex, year, and class of marine habitat were fixed factors. Percentages were arcsine transformed. Interactions between individuals and dependent variables were examined, and only significant interactions are reported in the text. All statistical tests were performed with Statistica 7.1. Effects of year, sex, and age class were likewise tested systematically in all analyses and are indicated only when significant ($P < .05$). Mean values are given ± 1 SD unless otherwise stated.

Results

Foraging Parameters and Prey Capture

The mean duration of foraging trips was 67.8 ± 23 h (range 8.9–95.6, $n = 27$), with a mean total distance covered per trip of $2,369 \pm 1,210$ km (range 319–4,710, $n = 17$) and a mean maximum foraging range of 508 ± 331 km (range 71–1,094, $n = 23$). On average, birds spent $55.7\% \pm 16.8\%$ (range 21.0–90.1, $n = 27$) of the foraging trip in flight, with an average flight speed of 56.6 ± 4.1 km h⁻¹. Wandering albatrosses foraged over oceanic waters as well as over neritic waters of the Crozet shelf and neighboring shelves (fig. 1). Overall prey ingestion rate was 60.1 ± 34.8 g h⁻¹ (range 9.5–135.1) and was similar between the two environments. The rate of mass gain, that is, the difference between body mass at departure and body mass at return to the nest, was 14.9 ± 28.7 g h⁻¹ (range -2.5–126, $n = 24$). The majority of prey by number (71.8%) and by mass (75.0%) was caught during the outward part of the trip, as opposed to the return phase.

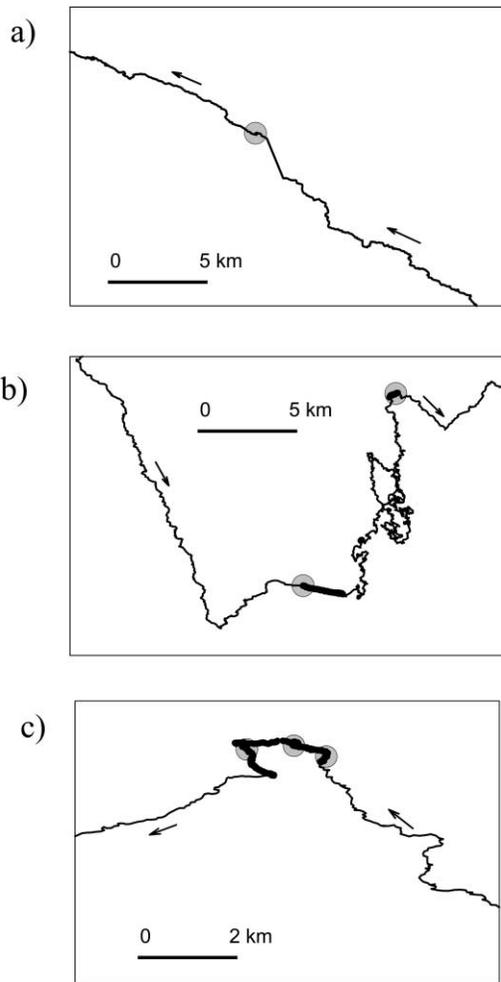


Figure 2: Three examples of small-scale foraging movements of wandering albatrosses. The thin line indicates the path in flight, the thick line or black dots when the bird is drifting and sitting on the water, and the gray dots prey capture. *a*, Foraging in flight; the prey is captured just after landing, with no change in sinuosity or flight direction after a prey capture. *b*, Foraging in flight, but the bird changes its sinuosity after the prey capture. *c*, Sit and wait; prey are captured when the bird is drifting on the sea surface.

Foraging Tactic

Wandering albatrosses clearly used two distinct modes of foraging: (1) an active search, where the prey was captured within a few seconds after landing, indicating that the bird had spotted the prey in flight, hereafter called “foraging in flight,” and (2) a “sit-and-wait” strategy, where the bird was sitting on the water for more than 10 min before prey was caught (fig. 2). Fifty-two percent of prey were caught after being detected in flight, while the rest were caught when the bird was sitting on the water (sit and wait), but only 17.3% of the total mass captured was captured by sit

and wait because prey captured by sit and wait were smaller (mixed-effects ANOVA: $F = 9.0$, $df = 1, 25$, $P = .026$; 137.7 ± 212.9 vs. 593.1 ± 787.5 g). The overall rate of prey capture of the sit-and-wait mode was 28.2 ± 36.6 g h^{-1} spent on the water (range 0–124), compared to 106.3 ± 76.0 g h^{-1} (range 7–220) for foraging in flight. Both strategies were used in similar proportions in oceanic and neritic waters and by males and females ($\chi^2 = 0.035$, $df = 1$, $P = .852$ and $\chi^2 = 0.007$, $df = 1$, $P = .934$, respectively), but sit and wait occurred mainly at night (74.4% of prey captures during sit and wait occurred at night; $\chi^2 = 18.9$, $df = 1$, $P < .001$). When foraging in flight, the rate of prey capture was nearly significantly higher but also much more variable in neritic than in oceanic waters (mixed-effects ANOVA: $F = 5.4$, $df = 1, 15$, $P = .061$; 150.3 ± 210.6 vs. 81.2 ± 68.2 g h^{-1}). The distribution of the distance between prey indicates that prey capture was not significantly different from a negative exponential (fig. 3; $\chi^2 = 6.2$, $df = 3$, $P = .092$), suggesting a tendency for birds to encounter some of the prey in aggregations, as indicated by feeding events occurring within 1 km of each other. However, most prey capture occurred as isolated events (70.5%). Isolated prey represented 92.4% of the total mass of prey captured, because prey in patches were much smaller than isolated prey (mixed-effects ANOVA: $F = 9.5$, $df = 1, 122$, $P = .01$; 92.2 ± 51 vs. 457.5 ± 700.2 g). All prey caught in patches, that is, at distances of <1 km, were caught using a sit-and-wait technique ($\chi^2 = 55.4$, $df = 1$, $P < .001$).

ARS and Prey Capture

ARS zones detected by the FPT method were found in all except one individual, with the radius of ARS zones varying from 5 to 90 km (fig. 4), and 51.9% of ARS detected was nested into larger-scale ARS. ARS occurred mainly

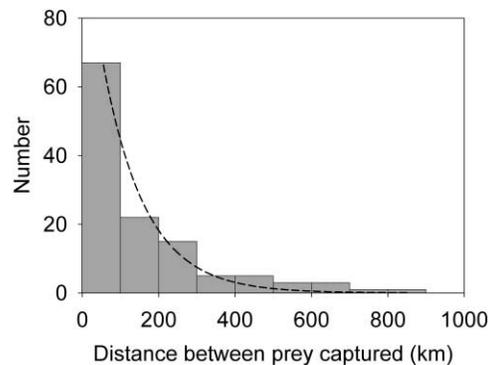


Figure 3: Frequency distribution of the distance between preys captured by wandering albatrosses.

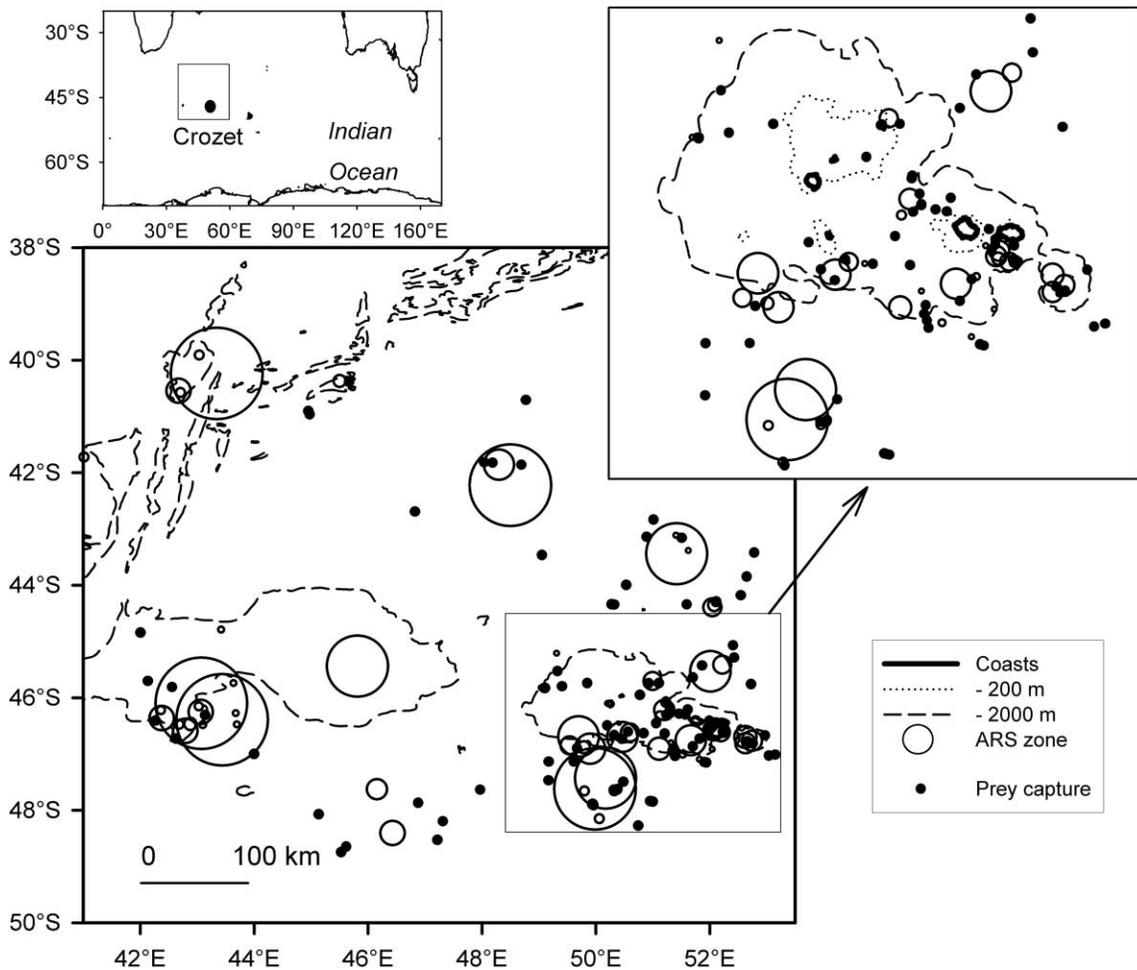


Figure 4: Map of the southwestern Indian Ocean showing the location of prey captures (filled circles) and zones of area-restricted search (open circles), with an enlargement of the Crozet shelf area sector. Inset shows the location of the study area in the Indian Ocean.

over shelf edges (72.2%) but also over oceanic waters (fig. 4). ARS zones were smaller over the nearby Crozet shelf than over oceanic waters and distant shelves (fig. 4; $F = 4.8$, $df = 1, 21$, $P = .043$; 16.2 ± 9.2 vs. 36.4 ± 32.4 km). The rate of prey capture when foraging in flight was similar inside ARS zones when compared with outside ARS zones ($F = 5.4$, $df = 1, 15$, $P = .723$; 102.2 ± 87.1 vs. 114.5 ± 224 g h^{-1}). Younger birds appeared to have larger ARS zones (31.1 ± 25.2 vs. 19.5 ± 10.2 km for older birds), mainly because they were the only ones to have ARS zones of large size (>60 km) when compared with older birds (mixed-effects ANOVA: $F = 2.7$, $df = 1, 20$, $P = .0210$). Young birds also appeared to have a larger number of nested ARSs compared to old birds, with small ARSs nested within large ARSs ($\chi^2 = 4.9$, $df = 1$, $P = .027$).

Birds spent $23.0\% \pm 14.0\%$ of their foraging time in

ARS zones, and $25.4\% \pm 17.4\%$ (range 0–54.6) of the total mass of prey was captured within an ARS zone, the rest being captured in straight-line flight, suggesting that most prey were captured opportunistically. ARS behavior started after a prey capture in only 12.5% of the cases, and the size of the ARS zone was not influenced by whether ARS occurred after prey capture ($F = 1.1$, $df = 1, 15$, $P = .381$). Prey were captured in similar proportions by either sit and wait or foraging in flight both inside and outside ARS zones ($\chi^2 = 0.001$, $df = 1$, $P = .975$).

To examine whether birds changed sinuosity after they captured a prey item, we considered only foraging in flight and excluded captures by sit and wait. Overall, there was a $21.1\% \pm 47.1\%$ increase in sinuosity 2 min into flight after prey capture (Wilcoxon test for paired samples: $Z = 2.9$, $P = .0037$), only $6.1\% \pm 18.4\%$ 10 min after ($Z = 1.9$, $P = .062$), and no increase 20 min later

($0.7\% \pm 23.0\%$, $Z = 0.4$, $P = .715$). The increases in sinuosity were significant only within ARS zones, as opposed to outside them, and 2 or 10 min after the capture of large prey, as opposed to small prey (fig. 5). Outside ARS zones, there was a tendency, but not a significant one, for an increase in sinuosity 2 and 10 min after capture of a large prey ($P = .061$ and $P = .070$, respectively; fig. 5).

Discussion

Understanding the rules governing foraging in a patchy environment is fundamental for developing realistic models of how animals behave in the wild and how they will respond to either climatic or anthropogenic change. In its use of high-precision GPS and loggers recording prey capture, this study provides the first multiscale investigation of the foraging strategy of a marine predator and how it reacts to prey capture. It becomes possible to link behavioral decisions to scale-dependent processes, that is, to combine behavioral ecology and landscape ecology, an approach that has been difficult to undertake so far (Lima and Zollner 1996).

Prey Distribution and Foraging Tactics

The use of ARS is expected to occur in patchy environments (Kareiva and Odell 1987) and probably at high prey densities within patches. Wandering albatrosses feed on squid species whose distribution is generally considered to be patchy, although few studies are available to validate this assumption (Cherel and Weimerskirch 1999). The distribution of distances between prey items caught by albatrosses suggests that the prey indeed have a patchy distribution, with large distances between patches (average distance between prey items 142 ± 185 km). To search for their prey, wandering albatrosses use two widely recognized modes of foraging (Pianka 1966), sit and wait and foraging in flight (Weimerskirch et al. 1997). The least productive mode is the sit-and-wait technique because it allows the capture of a limited amount of energy, less than three times the energy per unit of time, compared to foraging in flight. The energetic costs of sitting on the water are one and a half times lower than those of foraging in flight (Weimerskirch et al. 2000). Because of the use of cost-effective dynamic soaring (Weimerskirch et al. 2000), the efficiency (ratio of energy gained over energy spent) of foraging in flight is therefore about three times that of sit and wait. This result concurs with models predicting that a moving predator should always have a higher encounter rate compared with sit-and-wait predators (for a model, see Werner and Anholt 1993). However, it is the total amount of energy gathered rather than the encounter rate that is higher in the wandering albatross. Other pred-

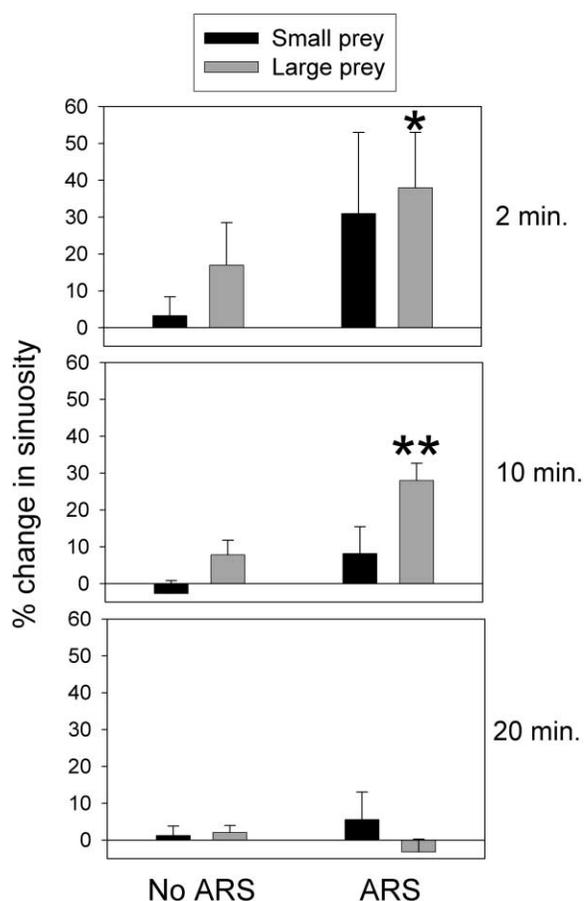


Figure 5: Change in sinuosity (± 1 SE) during foraging in flight, as the percentage of the change in sinuosity 2, 10, and 20 min before and after a prey capture, outside and inside an area-restricted search zone, and after the capture of small and large prey. The significance of the change for each case was tested by a Wilcoxon test for paired samples (*one asterisk* = $P < .01$; *two asterisks* = $P < .001$).

ators switch foraging mode according to factors such as spatial variation in prey abundance (Hirvonen 1999) and interspecific competition (Fausch et al. 1997). In wandering albatrosses, the sit-and-wait strategy is likely to be a secondary tactic used to capture small prey, mainly at night, when visual cues may be more limited. It is also used mainly over the shelf edges, possibly because different squid families occur there (Cherel and Weimerskirch 1999) and can be more easily captured at night by using this technique.

Scale-Dependent Foraging Strategies

The sit-and-wait strategy appears to be used for prey that are clustered in small-scale patches and for which foraging in flight would not be cost effective because it would re-

quire a very high turning rate and successive landings and take-offs, which are energetically very costly in albatrosses (Weimerskirch et al. 2000; Shaffer et al. 2001). At a larger scale, the most efficient mode appears to be foraging in flight, where birds move rapidly along a relatively straight route and capture prey just after it has been located.

It is during foraging in flight that a predator such as the wandering albatross is expected to modify its search pattern according to recent foraging success (Fauchald 1999). A previous study using GPS data and fractal analysis has suggested that wandering albatrosses use a scale-dependent hierarchical adjustment of movement patterns (Fritz et al. 2003), but it was not then possible to relate changes in movement pattern to prey capture. ARS zones are estimated to range between 5 and 90 km in radius and are particularly small over the Crozet shelf in the vicinity of colonies. Only young birds appeared to use large-scale ARS zones (60–90 km) that have nested smaller-scale ARS zones. This difference in behavior between age classes suggests that younger birds may have different foraging strategies, perhaps resulting from a poorer knowledge of the foraging habitat just around the breeding grounds that leads them to use large-scale ARS before moving to smaller-scale ARS. This difference has, however, no effect on the foraging success of young birds compared with older birds (Weimerskirch et al. 2005; this study).

Adjustment of Movement in Relation to Prey Capture

In contrast to predictions from models, during foraging in flight, prey capture failed to induce ARS behavior in most cases (only 12% of the events were followed by ARS). Thus, it appears that ARS is not driven by the experience of prey capture. ARS is often associated with the presence of the shelf edge, indicating that birds are probably able to recognize this feature because some cues, such as the color of the sea or odors (Nevitt 2000), are used. Previous knowledge of the foraging zone could also be used because individual wandering albatrosses are known to successively visit the same sector over shelf edges (Weimerskirch et al. 1993). In contrast, over oceanic waters, birds do not return to the same area from one trip to the next (H. Weimerskirch, unpublished manuscript), indicating that prey patches there are not stable in space or time and that other cues likely play a role in stimulating birds to start ARS. In particular, the presence of congeners, other seabirds feeding, or subsurface predators may indicate the presence of potential prey and induce birds to start an ARS (Silverman et al. 2004).

When looking at the overall pattern of movement, we find it clear that in this predator, the travel paths over enormous distances to find prey are generally straight (ARS zones represent only 23% of the foraging time). The use

of a straight movement over long distances appears to be particularly efficient because most prey are caught at this time and not during ARS. These data stand in strong contrast to the general view of the role of ARS for foraging animals (Kareiva and Odell 1987) but may be specific to this particular predator. However, using a generic model, Zollner and Lima (1999) predicted that straight movements are probably the most efficient way to search efficiently for prey over large scales. Thus, what has generally been considered to be a commuting phase, where birds fly in a relatively straight line, is when most prey are caught, meaning that this type of movement is not opportunistic but is rather the main search strategy with the highest efficiency for large-scale foragers.

So why do birds spend 23% of their time in ARS? Birds have similar rates of prey capture inside or outside ARS zones, suggesting that predictability is higher inside ARS zones. In addition, the knowledge of particular environments with previous good foraging success, such as over a shelf edge, would induce birds to restrict their movements in some areas. This could be why ARS is more common over shelf edges. The capture of prey would not be the cause for starting an ARS, but rather the knowledge of the environment, or the detection of indexes, such as the presence of congeners or other predators, would be the main factors inducing ARS. The constraint imposed by central-place foraging could also be an additional factor in these large-scale foragers, forcing them to restrict their movements at some stages. In particular, the brooding period is energetically very constraining for pelagic seabirds (Ricklefs 1983), and it is the only period when wandering albatrosses lose mass (Weimerskirch and Lys 2000). Birds have to return rapidly to the nest, restricting their movements to the relative proximity of the colonies and extensively using shelf edges. During incubation, when birds are foraging farther away from colonies and rarely foraging over the shelf edge, they move rapidly in straight lines during extended periods over oceanic waters but still use ARS zones that are located at greater distances from colonies (Pinaud and Weimerskirch 2005).

Prey predictability is generally assumed to be higher at larger than at smaller scales (Wiens 1989). Hunt et al. (1999) predicted that, for this reason, past experience and orientation are expected to play major roles for marine predators when adjusting their searching movements at large scales. In contrast, at small spatial scales, immediate prey encounter rate is expected to play a major role for these predators when adjusting their searching movements (Hunt et al. 1999). In wandering albatrosses, prey capture is not followed by ARS behavior at a medium or coarse scale or by a systematic increase in sinuosity at a fine scale. Prey capture induced an increase in sinuosity within ARS

zones when a large prey was captured but only during a limited period of time (<20 min). This result supports the hypothesis that highly sinuous paths that would make patch reencounter quite likely could be used by animals departing from high-quality patches. Models predict that, generally, trip displacement after a prey encounter is conditioned on patch quality (Walsh 1996). Here, we show that after a prey capture, birds return to a sinuosity similar to that before prey encounter within 20 min; that is, the increase in sinuosity is used to increase search effort to find other prey only near the prey caught.

Conclusions

This study indicates that a seabird foraging over large-scale habitats does not behave as predicted by models that have often been developed from observations of insects or small mammals in controlled situations, that is, over small scales. Because we are dealing with a fast-moving pelagic seabird, the generalization of our conclusions to other animals will have to be tested in the future. Animals moving over large scales face different constraints; in particular, they use scale-dependent adjustments of their movements. The navigation, learning abilities, and memory of these long-lived animals and their related ability to consistently use the same large-scale areas year after year during their entire life span (e.g., Weimerskirch et al. 1985; Weimerskirch and Wilson 2000) imply that these animals probably have a good knowledge of their environment that has been learned during immaturity and successive breeding experiences. In these animals moving over large scales, large-scale ARS is not used as an answer to prey capture but rather as a scale-dependent adjustment to the environmental conditions. Results from this study suggest that, in wandering albatross, ARS is closely linked not to the experience of prey capture but rather to features in the environments (neritic vs. oceanic waters), features particular to shelf breaks or seamounts (odor or visual cues), and the activity of other animals (see, e.g., Silverman et al. 2004). Birds make only fine-scale adjustments in response to prey capture in areas of high yield. The results of this study underline the importance of empirical data in better understanding the rules governing behavioral decisions in foraging animals because previous models were developed for small-scale, short-lived animals and probably cannot be directly applied to large-scale, long-lived animals with high cognitive capabilities.

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