

PLUMAGE POLYMORPHISM AND
KLEPTOPARASITISM IN THE ARCTIC SKUA
STERCORARIUS PARASITICUS

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Jones T. 2002. Plumage polymorphism and kleptoparasitism in the Arctic Skua *Stercorarius parasiticus*. *Atlantic Seabirds* 4(2): 41-52. *The Arctic Skua Stercorarius parasiticus is polymorphic, expressing a roughly clinal variation in plumage from the northern to the southern end of its breeding range. It has been suggested - but never confirmed - that the maintenance of this polymorphism may be related to their role as specialist kleptoparasites of other birds, through either predator apostatic selection, or selection for cryptic advantage. The southern breeding population of Handa Island, Scotland, was studied during the summer of 2000. Various aspects of 1421 attacks on Common Guillemots *Uria aalge* were recorded, and tested for differences in behaviour and outcome between the morphs. No differences were found in relation to chase success rates, methods of attack, or the response of their victims. It is concluded that the polymorphism of this species is unrelated to its kleptoparasitic behaviour. Some other possible explanations for the plumage variation are briefly discussed.*

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INTRODUCTION

From an evolutionary point of view, Arctic Skuas *Stercorarius parasiticus* are of particular interest for two main reasons. Firstly, they are polymorphic in plumage; most birds are either 'dark-phase' individuals (covered in dark feathers), or 'pale-phase' individuals (with light underparts), although some 'intermediates' (with fewer light feathers) do occur. Examples of all these morphs are often found within single populations. Secondly, they show an unusually high degree of dependence on kleptoparasitism for attaining food; indeed, this may be the only species of bird capable of surviving all year round using this feeding technique alone (Furness 1987). It has been suggested (Amason 1978; Caldow & Furness 1991) that there may be an ecological relationship between these two aspects of their biology, and that this may explain how and why this polymorphism is maintained. On the other hand, a number of other mechanisms have been suggested, relating to sexual selection, timing of breeding and heat loss.

The polymorphism is expressed in different ratios in different populations. Ornithologists have been counting numbers of the different phenotypes in different breeding grounds for over a century, and reviews of these data (O'Donald 1983; Furness 1987) demonstrate that the frequencies of melanic birds form a cline roughly from the northern to the southern end of their

range. On Bear Island, Spitzbergen, fewer than 1% of the birds were melanic in 1943, whereas on Shetland, the frequency remained fairly stable from 1963-1975, at about 75%.

Feeding behaviour also varies in relation to geographical location. For example, to the north of their range, many Arctic Skuas breeding inland on Arctic tundra are generalised terrestrial predators, feeding on birds, eggs and berries. At lower latitudes, including at the site where the present study was conducted, populations are much more dependent on kleptoparasitism. Here, skuas pursue auks and other seabirds, sometimes making physical contact, until either the victim has dropped whatever food it is carrying, or has escaped. The skua collects the food in mid-air or from the surface of the ocean, either for its own consumption, or to present later to its offspring or mate.

Two hypotheses have been forwarded linking plumage polymorphism to kleptoparasitism. Firstly, the melanic morph may be a form of 'aggressive camouflage' for kleptoparasitic birds (Phillips 1962). That is to say, certain plumage may render the skua less conspicuous to its victim. As the polymorphism is expressed ventrally in the Arctic Skua, attacks should occur more frequently from above. The discovery of Furness (1978) that approaching close to a victim before being detected increases the probability of a successful attack, is consistent with this idea. Andersson (1976) found that skuas attempt more chases in conditions of poor visibility, which could be related to an increase in the effectiveness of their camouflage. The incidence of less kleptoparasitism to the north of their range, where there is a higher proportion of pale-phase birds, is also compatible with the 'aggressive camouflage' hypothesis.

Secondly, there is the 'predator apostatic selection', or 'avoidance-image', theory (Payne 1967; Paulson 1973). "Intelligent" prey with good visual acuity, such as auks, may use search images to spot familiar potential predators. This could lead to selection pressure in favour of the rarer morph in a given population. Amason (1978) found that the rarer light birds in his study population were more successful in attacks than the more common dark birds, but O'Donald (1983) tested the data and found that the result was not statistically significant. Furness & Furness (1980) also presented data that showed no significant differences in chase success rates between birds of different plumages. However, Caldow & Furness (1991) later argued that they had presented evidence, again from Shetland, which supported the hypothesis that "the arctic skuas' plumage polymorphism is maintained, at least in part, by differential chase success rates brought about through apostatic selection". The matter is far from resolved, and the possibility remains that sexual selection or some other factor may be key to the distribution of the different morphs.

In the light of this uncertainty, the aim of this study was to explore

further the idea that kleptoparasitic behaviour is in some way associated with the species' polymorphism. Data were collected on a large number of chases by both dark- and light-phase birds, and analysed for differential results between the two morphs. If aggressive camouflage were involved, we would expect to find a correlation between the chase success rate of each morph, and the environmental background from which these attacks were launched. However, if predator apostatic selection were a function of the skuas' polymorphism, we would predict a greater chase success rate for the rarer morph within a population, in this case the pale-phase birds.

METHODS

Handa is a small island of about 3 km² lying 1 km off the north-west coast of Scotland, at a latitude of 57°N. In the spring and summer, its dense breeding cliffs host approximately 75,000 pairs of Common Guillemot *Uria aalge* and 7500 pairs of Razorbill *Alca torda*, as well as numerous Atlantic Puffins *Fratercula arctica*, Black-legged Kittiwakes *Rissa tridactyla*, Northern Fulmars *Fulmarus glacialis*, and European Shags *Phalacrocorax aristotelis*. On the interior of the island, on territories covered with *Calluna* moorland, Arctic Skuas rear their young. In 2000, there were 40 Apparently Occupied Territories.

Two ecological aspects of Handa's breeding Arctic Skuas are worth noting. Firstly, there is an unusually high proportion of light-phase birds, given the position of the island at the southern end of the species' range. On 12 July 2000, there were 55 dark-phase and 24 light-phase birds present on the island (69.6% and 30.4% respectively). This compares with ratios of light-phase birds on Shetland, to the north-east of Handa, of less than 20% (Furness 1987; Phillips & Furness 1998). Nevertheless, the light-phase birds of Handa still represent the rarer morph, making them good candidates for testing the apostatic selection theory. Secondly, throughout the breeding season, the entire population displays an extremely high dependence on kleptoparasitism, mostly on Common Guillemots. Other kinds of feeding behaviour are very rarely observed in this well-monitored population (Scottish Wildlife Trust 1975-2000; Uwe Stoneman pers. comm.).

From mid-June until mid-July, chases by Arctic Skuas of auks, and occasionally other species, were recorded over a total of 23 days. Observations were made from the island using binoculars and the naked eye, and therefore all the recorded chases occurred over the sea within approximately 800 m of the breeding cliffs. In order to distinguish between the different plumages of the skuas, I employed the simple and very practical criteria laid out in the Seabird Monitoring Handbook (Walsh *et al.* 1995). Thus there are two categories of birds: 'pale-phase' or 'light-phase' birds (these two terms are interchangeable)

Table 1. The total number of chases attempted and the rates of success achieved by dark-phase and light-phase Arctic Skuas on Common Guillemots, and on all other species (df = 1 for all tests; n.s. = not significant).

Tabel 1. Aantal aanvallen en het percentage succesvolle aanvallen voor donkere en lichte fase Kleine Jagers op Zeekoeten en andere zeevogels.

	Dark		Light		χ^2	P
	n	% success	n	% success		
Common Guillemot	920	10.4	501	10.58	0	n.s.
All other species ¹	59	5.08	33	3.03	0.2	n.s.

¹Comprising Razorbill, Atlantic Puffin, Black-legged Kittiwake and Northern Fulmar.

have light-coloured underparts; 'dark-phase' birds comprise all the others, including uniformly dark birds and all the typical intermediate birds, which are dark apart from pale neck or ear-covert feathers. For each chase, the following details were recorded:

- date;
- cloud cover: 0% (blue sky), 25%, 50%, 75% or 100%;
- colour of the cloud cover: all white, all grey, or a mixture of white and grey;
- wind force, using the Beaufort Scale;
- plumage of the attacker: 'light' or 'dark';
- species of the victim;
- estimated distance from the island to the position of the attacker when the chase was initiated;
- direction of the attack i): from above, from below, or from level flight;
- direction of the attack ii): from in front, from behind, from the side - or from directly above (not recorded for first 7% of observed chases);
- duration of the chase: <5, 5-10 or >10 seconds;
- escape response of the victim: to fly downwards and then resume level flight, to fly into the sea, or to continue level flight (changing direction and/or accelerating);
- whether or not the attacker made physical contact with its victim; and
- the outcome: success (the victim drops its fish) or failure (the victim drops nothing).

RESULTS

In total, 1513 chases were recorded, of which 1421 were attacks on Common Guillemots. All of the results that follow, with the exception of the chase success rates on the other targeted species (Table 1), refer to interactions between the Arctic Skua and the Common Guillemot. For the other species attacked, the sample sizes were too low to allow meaningful analyses. A few chases were recorded by more than a single bird (including some attacks on a Peregrine *Falco peregrinus*), but these were not included in the final data. To investigate a possible association between the skuas' polymorphism and their kleptoparasitic behaviour, the chases by light- and dark-phase birds respectively were analysed for differences in their overall success rates, the direction of their attacks in relation to their victims, and the response of their victims to attack.

Table 2. The total numbers and success rates of attacks by all Arctic Skuas according to the direction in relation to the victim from which the attack was initiated (df = 2 for both tests; n.s. = not significant).

Tabel 2. Aantal aanvallen van Kleine Jagers en het succespercentage in relatie tot de aanvalsrichting: van boven, op gelijke hoogte en van onder.

	Above	Level	Below	χ^2	<i>P</i>
No. of chases	1005	374	42		
% of all chases	70.72	26.32	2.96	747.81	0
% successful	10.85	9.89	7.14	0.64	n.s.

Chase success rates The overall success rates for the entire Arctic Skua population were 10.49% for chases of guillemots (n=1421), and 4.35% for chases of all other species (n=92). There was little difference between the overall chase success rates of dark- and light-phase birds. In fact, in the case of chases of Common Guillemots (the only victim species with a meaningful sample size), the overall success rates were extremely similar (Table 1).

Direction of attack Because guillemots are bifocal predators of fish (Nettleship & Birkhead 1985), their vision is limited to the front and to the side; they cannot see behind. We might therefore expect a predator-prey evolutionary arms race to have led the kleptoparasitic Arctic Skua to take advantage of this by attacking most often from behind its victim. However, this hypothesis is not borne out by the results of this study. Of all the attacks observed, 27.02% were from behind, compared with 29.53% from the front and 41.93% from the side. Although the success rate was higher from behind (12.11%) than from other directions (11.25% from the side, and 7.99% from the front), none of the differences were statistically significant (front/behind: $\chi^2 = 2.87$, df = 1, *P* = 0.090).

Since the Arctic Skua's polymorphism is expressed mostly on the underside of its body, most attacks might be expected to occur from above the victim if there were any relationship between plumage polymorphism and kleptoparasitic success. In this study, it was found that the majority of attacks were indeed from above (Table 2). Also, attacks from above resulted in a slightly higher success rate than attacks from level flight, and although the difference was not statistically significant, it does represent a potential difference in energy gain for the attacking birds of approximately 10%. Very few attacks were attempted from below and the success rate was relatively poor, which is compatible with the idea that the plumage of the attacking bird may affect both direction of attack, and chase success rate. However, to clarify this hypothesis, we need to consider the respective success rates for each bird. In accordance with the predator apostatic selection theory, it is predicted that since

Table 3. The numbers, proportions and success rates of attacks by dark-phase and light-phase birds from above, level with and below the victim (n = 1421; df = 1 for all tests; n.s. = not significant).

Tabel 3. Aantal en succespercentage van aanvallen door donkere en lichte fase Kleine Jagers in relatie tot de richting van waaruit het slachtoffer werd belaagd: van bovenaf, op gelijke hoogte en van onderen af.

		Dark	Light	χ^2	P
Above	No. of attacks	689	316		
	% of all attacks	74.89	63.07	6.92	< 0.01
	% successful	11.47	9.49	0.71	n.s.
Level	No. of attacks	205	169		
	% of all attacks	22.28	33.73	9.24	< 0.01
	% successful	7.32	13.02	2.76	n.s.
Below	No. of attacks	26	16		
	% of all attacks	2.83	3.19	0.04	n.s.
	% successful	7.69	6.25	0.03	n.s.

pale-phase birds constitute the rarer morph in the Handa population, they should experience greater success when attacking from above than the dark-phase birds. In fact, the success rates were similar for each morph (Table 3), that of the dark-phase birds being slightly higher, but not significantly different.

Finding evidence for the skuas' plumage acting as a form of aggressive camouflage against their victims required testing for a correlation between the success rate for each morph and the background from which it was attacking. Most of the chases observed took place from above (Table 2), and very few (1.65%) occurred within 50 m of the breeding cliffs. Therefore, the most likely cryptic advantage to be gained in this instance would arise from the skua matching its underparts to the colour of the sky, i.e. by attacking from above. Moreover, because of the limits to the guillemot's vision already discussed, camouflage could only have been a function of chase success when the skua was attacking from the front, from the side, or from directly above. Table 4 shows the results, for each morph, of these types of chases. The total number of attacks from these directions was 584, of which 381 were by dark-phase birds, and 203 were by pale-phase birds. There was very little difference between the success rates of each morph, and both were close to the overall average of about 10.5%.

Considering the dark phase birds, it was hypothesised that if they were benefiting from a cryptic advantage, they should have a higher success rate than the pale-phase birds when attacking against a background of grey clouds, especially since the 'dark' birds of this study included some intermediates. Only chases occurring under a sky with more than 50% cover of grey clouds were

Table 4. Numbers, proportions and success rates of attacks by each Arctic Skua morph, under different environmental conditions, which were initiated either from directly above, from above and in front of, or from above and to the side of the victim ($n = 1314$; $df = 1$ for all tests; n.s. = not significant).

Tabel 4. Aantal en succespercentage van aanvallen door donkere en lichte fase Kleine Jagers in relatie tot de bewolking voor aanvallen die van boven werden ingezet

Cloud cover	Dark		Light		χ^2	P
	n	% success	n	% success		
All conditions	381	10.5	203	11.82	0.19	n.s.
Grey ¹ sky	170	7.65	71	7.04	0.02	n.s.
White ¹ sky	54	11.11	32	12.5	0.03	n.s.

Table 5. The numbers, proportions and success rates of chases by all Arctic Skuas and by each morph, in relation to the duration of the chase ($n = 1421$; $df = 1$ for all tests; n.s. = not significant).

Tabel 5. Aantal, aandeel en succespercentage van aanvallen voor alle Kleine Jagers en per kleurfase in relatie tot aanvalsduur.

Length of chase (seconds)		Total	Dark	Light	χ^2	P
< 5	No. of chases	1221	788	433		
	% of all chases	85.93	85.65	86.43	0.01	n.s.
	% successful	11.00	10.79	9.70	0.29	n.s.
≥ 5	No. of chases	200	132	68		
	% of all chases	14.07	14.35	13.57	0.12	n.s.
	% successful	10.40	8.33	16.18	2.21	n.s.

included in the analysis, and these conditions prevailed for part or all of 12 of the 20 observation days. However, although chases of this kind accounted for nearly 20% of all the dark birds' chases, compared with about 16% of all the light birds' chases, the success rates for both morphs were very similar and, at about 7%, relatively poor.

Similarly, I hypothesised that a key test of the pale morph's cryptic advantage would be its relative success rate of chases from above (and from the front, from the side or from directly above), against a background of white clouds. Again, only cloud cover greater than 50% was considered. These conditions were less common, prevailing on four of the 20 observation days. Probably as a consequence, chases under a white sky comprised only 7.16% of all the light birds' chases, and a similar 6.23% of all the dark birds' chases. The success rate for the light birds was 12.50%, only marginally higher than their overall success rate, and close to the dark birds' success rate under these conditions of 11.11%.

Table 6. Numbers of Apparently Occupied Territories (AOT), dark-phase birds and light-phase birds (and percentage of the total population) present on Handa during selected breeding seasons since 1975 (From Scottish Wildlife Trust 1975-2000).

Tabel 6. Aantal kennelijk bezette territoria (AOT), donkere fase en lichte fase Kleine Jagers (en aandeel in de gehele populatie) op Handa gedurende een aantal broedseizoenen sinds 1975 (naar Scottish Wildlife Trust, 1975-2000).

Year	AOT	Dark (%)	Light (%)
1975	2	3 (75.0)	1 (25.0)
1980	13	15 (57.7)	11 (42.3)
1985	36	50 (69.4)	22 (30.6)
1996	29	39 (67.2)	19 (32.8)
1997	30	45 (77.6)	13 (22.4)
1998	32	43 (69.3)	19 (30.7)
1999	35	47 (69.1)	21 (30.9)
2000	40	55 (69.6)	24 (30.4)

Response of guillemots to attack Finally, the outcomes of attacks were analysed with regard to the duration of the interactions. Chases were divided into those lasting less than 5 seconds, and those lasting 5 seconds or longer. I hypothesised that there may be a relationship between the length of the chase, and the response time of the guillemot to attack. A shorter chase may correspond to a more successful evasion of the attacking skua, and this may be a function of the speed at which the victim is able to recognise its attacker. If so, a cryptic advantage held by the attacker, or predator image-avoidance by the victim, would have an effect on such a relationship. There was some limited evidence in support of this hypothesis. The most common evasion tactic by guillemots was to fly down towards the sea (64.74% of all chases), and the success rate for all skuas when the guillemots responded in this way was 9.42%, slightly lower than the success rate for all chases of 10.49% (but not significantly different: $\chi^2 = 0.64$, $df = 1$, $P = 0.425$). It is interesting to note that while this type of response resulted from 64.74% of all chases, it occurred in 75.35% of all the chases lasting less than 5 seconds. Thus, the possibility arises of a correlation between a shorter chase and a lower success rate, due to more rapid recognition of the attacker by the victim. Crucially, if this variation in recognition time were a function of the attacker's plumage, we would predict differential chase success rates between the two morphs in relation to the length of the chase.

However, the results confirm that this was not the case (Table 5). The total success rates, for chases shorter than 5 seconds and for those that lasted

longer, were very similar, and close to the overall success rate. Moreover, there were no significant disparities in chase success rate between the two morphs. For chases under 5 seconds, which constituted approximately 85% of the total number, the success rates for both light- and dark-phase birds were close to the overall average. For chases lasting 5 seconds and longer, the light-phase birds had a higher success rate, but the sample size was only 68 and the difference was not statistically significant. Once again, analysis of the data has failed to reveal any significant differences in either kleptoparasitic behaviour or outcome between the two morphs.

DISCUSSION

One of the patterns that clearly emerges from this study is the consistent success rate achieved from attacks on Common Guillemots. Whether the attacks are categorised according to the direction of the attack, the prevailing cloud cover or the escape responses of their victim, the chases resulting in the attainment of fish repeatedly constitute about 10% of the total. The only exceptions to this trend are those relatively small categories of chase where the sample size is low, for example chases initiated from below the victim (Table 3). Whenever the sample size is greater than 100 (whatever the category of chase), the success rate approaches 10%. It thus appears that 100 is a minimum sample size for obtaining valid results pertaining to Arctic Skua chases. This analysis is consistent with a previous study on Shetland (Caldow & Furness 1991), which also found that success rates for Arctic Skuas attacking Common Guillemots were approximately 10% whenever the analysis included more than 100 chases.

The second pattern to emerge - and the most important in the context of the aims of this study - is that of the consistency in feeding success between the two morphs. Again, no matter how the attacks are categorised, the success rates for both light- and dark-phase birds are extremely similar. No significant differences were found between the morphs in terms of their chase success rates, whether overall or for particular methods of attack, nor in the responses of the guillemots. These findings are very similar to those of Paterson (1986), who detected no difference in the success rates of dark- and light-phase adults attacking gulls and terns.

According to the aggressive camouflage theory, because the dark-phase birds are more common in the Handa population this morph would have been selected for because it confers a cryptic advantage when attacking its victims. Andersson (1976) argued that dark plumage renders the Arctic Skua inconspicuous, and may be a form of camouflage *per se*. Alternatively, the dark-phase skuas could be using darker backgrounds from which to launch their attacks. However, no differences were found between the success rates of dark

and light morphs, either generally, or under those circumstances likely to lend cryptic advantage to attackers of a particular plumage. While dark-phase birds did attempt more chases from above their victims than light-phase birds, it is unclear why this was so, since they did not achieve a greater success rate. This was the case not only for chases under all environmental conditions, but also for chases against a potentially advantageous background of grey clouds. Equally, no cryptic benefit could be found for the plumage of the light-phase birds. The aggressive camouflage hypothesis is therefore not supported.

There is also no support in the results for the predator apostatic selection hypothesis; a greater success rate for the rarer pale morph would have been expected but this was not the case. Also, as their distinct plumage is most visible from directly below, it would have been expected that the light-phase birds would have attacked from above more often than the dark-phase birds, in order to maximise their chances of deceiving their victim. In fact, they employed this method of attack significantly less frequently than the dark birds, and their success rate was slightly lower. The evidence strongly discounts the use of fixed mental images by Common Guillemots to avoid their commonest attackers.

Rohwer (1983) pointed out that caution must be exercised in drawing conclusions from the results of relatively short-term studies. He argued that a result of no significant difference in chase success rates is not necessarily incompatible *per se* with either the aggressive camouflage hypothesis or the apostatic selection hypothesis, since selection pressures may be acting in opposite directions. If they were both a factor in natural selection of plumage types in a particular population, they could be selecting simultaneously for opposite morphs, and could effectively cancel each other out. However, the similarity of the results for both morphs, especially for those specific chases that ought to have resulted in advantage to one or other of the morphs according to these theories (Tables 3 and 4), diminish this possibility.

It is not certain whether the polymorphism of the study population is stable, since the existing data are limited and the colony is young and continues to expand (Table 6). However, the data do not suggest a current trend in favour of either morph. The results of a longer-term study of Arctic Skuas on Shetland indicate that natural selection may presently be favouring the melanic plumage of the dark-phase birds (Phillips & Furness 1998). This could have implications for the Handa population. Both locations are at the southern end of the species' breeding range, so it might be expected that the birds are subject to the same selection pressures. Also, they are separated by only 260 km of open ocean, so some degree of gene flow between the two populations might also be predicted.

The results presented are somewhat counter-intuitive, given the apparent clinal variation in plumage observed in this species from north to

south. Nevertheless, in order to enhance our understanding of this polymorphism, future study should perhaps focus on aspects of the Arctic Skua's life other than its kleptoparasitic behaviour. Some evidence has been found supporting the existence of assortative mating within a population (Phillips & Furness 1998), and this could be significant. Alternatively, other kinds of evolutionary pressures arising from sexual selection might be acting on the birds. Catry *et al.* (1999) argued that the reversed sexual size dimorphism found in this species could be a result of intrasexual competition for mates, and perhaps a similar explanation might hold for their plumage polymorphism. Furness (1987) noted that colour phase seems to be influenced by the sex of the individual. Finally, it is known that the Arctic Skua is preyed upon by at least one species, the Great Skua *Catharacta skua* (Furness 1977; Phillips *et al.* 1998; personal observations), but it is unknown whether birds of certain plumages are preyed upon preferentially.

In summary, this study found that the dark- and light-phase birds of a single population were extremely similar in all aspects of their kleptoparasitic feeding behaviour, and that their success rates - both overall and for each type of chase - were remarkably consistent. The body of evidence suggests that the existence of a range of plumages within a population of Arctic Skuas is unrelated to their kleptoparasitic behaviour. The evolutionary mechanisms underlying the polymorphism of this species remain little understood and are likely to be established through research into other aspects of their biology.

ACKNOWLEDGEMENTS

The Scottish Wildlife Trust granted me permission to undertake this study on Handa Island Nature Reserve, and to stay in their bothy. Dr. Ben Hatchwell of the University of Sheffield was generous with encouragement and advice. The warden of the reserve, Uwe Stoneman, provided some valuable suggestions and a wealth of knowledge of Handa's birdlife, as well as fine company.

KLEURFASEN EN KLEPTOPARASITISME BIJ DE KLEINE JAGER *STERCORARIUS PARASITICUS*

*De Kleine Jager kent een lichte en een donkere kleurfase, waarvan de onderlinge verhoudingen verschillen in de verschillende delen van zijn verspreidingsgebied. Lichte fase vogels zijn het talrijkst in arctische gebieden, terwijl in de zuidelijke broedgebieden, zoals in Schotland, veel vogels tot de donkere fase behoren. Het is vaak verondersteld, ofschoon dat nimmer werd aangetoond, dat de kleurfasen blijven bestaan vanwege hun betekenis bij het kleptoparasitaire gedrag van jagers. In gebieden waar veel voedsel bemachtigd wordt door kleptoparasitisme zouden veel donkere fase individuen voorkomen, terwijl in de arctische broedgebieden, waar lichte vogels domineren, bijna al het voedsel zelfstandig wordt gevangen. Donkere vogels zouden wegvallen tegen de achtergrond en daardoor in het voordeel zijn wanneer zij hun slachtoffers kozen en belaagden. Op het Schotse eilandje Handa, waar één van de meest zuidelijke kolonies van de Kleine Jager is gevestigd, werd het succes van lichte en donkere Kleine Jagers als kleptoparasiet bestudeerd in de zomer van 2000. In totaal werden 1421 aanvallen van voedsel aanbrengeende Zeekoeten *Uria aalge* bestudeerd, waarbij bijvoorbeeld de hoek van aanvallen (van onderen, van boven en op dezelfde vlieghoogte) en*

de mate van bewolking in ogenschouw werden genomen. Zo werd nagegaan of een donkere vogel bij zwaar bewolkt weer een grotere kans op succes had, of dat een lichte fase vogel bij een aanval van bovenaf bij een lichte lucht een betere kans maakte om zijn slachtoffer met succes te verrassen. Er werd echter geen enkel verschil tussen de beide kleurvarianten gevonden, zodat geconcludeerd wordt dat er geen relatie bestaat tussen de kleurfase en het succes als kleptoparasiet.

REFERENCES

- Andersson M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. *Ibis* 118: 208-217.
- Arnason E., 1978. Apostatic selection and kleptoparasitism in the parasitic jaeger. *Auk* 95: 377-381.
- Caldow R.W.G & Furness R.W. 1991. The relationship between kleptoparasitism and plumage polymorphism in the Arctic skua *Stercorarius parasiticus*. *Functional Ecology* 5: 331-339.
- Catry P., Phillips R.A. & Furness R.W. 1999. Evolution of reversed sexual size dimorphism in skuas and jaegers. *Auk* 116: 158-168.
- Furness B.L. & Furness R.W. 1980. Apostatic selection and kleptoparasitism in the parasitic jaeger: a comment. *Auk* 97: 832-836.
- Furness R.W. 1977. Effects of Great Skuas on Arctic Skuas in Shetland. *British Birds* 70: 96-107.
- Furness R.W. 1978. Kleptoparasitism by great skuas (*Catharacta skua* Brünn.) and Arctic skuas (*Stercorarius parasiticus* L.) at a Shetland seabird colony. *Animal Behaviour* 26: 1167-1177.
- Furness R.W. 1987. The skuas. T. & A.D. Poyser, Calton.
- Nettleship D.N. & Birkhead T.R. 1985. The Atlantic Alcidae. Academic Press, London.
- O'Donald P. 1983. The Arctic skua: a study of the ecology and evolution of a seabird. Cambridge University Press, Cambridge.
- Paterson A.J. 1986. Kleptoparasitic feeding by migrating skuas in Malaga Bay, Spain. *Ring and Migration* 7: 51-55.
- Paulson D.R. 1973. Predator polymorphism and apostatic selection. *Evolution* 27: 269-277.
- Payne R.B. 1967. Interspecific communication signals in parasitic birds. *American Naturalist* 101: 363-375.
- Phillips G.C. 1962. Survival value of the white colouration of gulls and other seabirds. Unpublished PhD thesis, University of Oxford, UK.
- Phillips R.A. & Furness R.W. 1998. Polymorphism, mating preferences and sexual selection in the Arctic skua. *Journal of Zoology* 245: 245-252.
- Phillips R.A., Furness R.W. & Stewart F.M. 1998. The influence of territory density on the vulnerability of Arctic skuas *Stercorarius parasiticus* to predation. *Biological Conservation* 86: 21-31.
- Rohwer S. 1983. Formalizing the avoidance-image hypothesis: critique of an earlier prediction. *Auk* 100: 971-974.
- Scottish Wildlife Trust. 1975-2000. Handa Island Nature Reserve, Warden's Annual Reports (available from Scottish Wildlife Trust Edinburgh).
- Walsh P.M., Halley D.J., Harris M.P., del Nevo A., Sim I.M.W & Tasker M.L. 1995. Seabird monitoring handbook for Britain and Ireland. JNCC, Peterborough.

FORAGING BEHAVIOUR OF NON-BREEDING POMARINE SKUAS *STERCORARIUS POMARINUS* IN THE NORTH SEA IN SUMMER

VOLKER DIERSCHKE & JAN-PETER DANIELS

Dierschke V. & Daniels J.-P. 2002. Foraging behaviour of non-breeding Pomarine Skuas *Stercorarius pomarinus* in the North Sea in summer. *Atlantic Seabirds* 4(2): 53-62. From late May to mid September 2000, the unusual event of a summer assemblage of up to 16 Pomarine Skuas occurred on the island of Helgoland (German Bight, North Sea). Most of the birds were immatures in second and third calendar-year, which moulted primaries, tail feathers and wing coverts. The Pomarine Skuas usually foraged by kleptoparasitism of Black-legged Kittiwakes *Rissa tridactyla* carrying food to the breeding colony. Success of attacks was higher with Black-legged Kittiwakes compared to other victims (e.g. Sandwich Tern *Sterna sandvicensis* and Arctic/Common Tern *S. paradisaea/hirundo*), placing Pomarine Skuas between Arctic Skuas *Stercorarius parasiticus* (preferably hunting terns) and Great Skuas *Catharacta skua* (unable to kleptoparasitise terns and attacking Black-legged Kittiwakes less often than Arctic and Pomarine Skuas do). When chasing Black-legged Kittiwakes, age of Pomarine Skuas and size of the hunting group (sometimes including Herring Gulls *Larus argentatus*) did not affect the success rate, but with larger group size the success per group member decreased. The unusual occurrence of a group of moulting Pomarine Skuas suggests that the sea around Helgoland holding many seabirds during the breeding season is usually under-exploited by skuas.

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INTRODUCTION

Because of their pelagic distribution, little is known about the foraging behaviour of skuas during the non-breeding season. Foraging at sea was studied intensively in Great Skua *Catharacta skua* and Arctic Skua *Stercorarius parasiticus* which breed in or close to seabird colonies and to a large degree depend on kleptoparasitism on seabirds like gannets, gulls, terns and auks (reviewed by Furness 1987a, 1987b). In breeding Pomarine Skuas *Stercorarius pomarinus*, foraging is more restricted to terrestrial habitats, where rodents are the most important prey (Glutz von Blotzheim & Bauer 1982). Furthermore, Pomarine Skuas occur in much lower numbers along the coastlines of northwestern Europe than Arctic Skuas (Meltøfte 1979; Platteeuw *et al.* 1994, Camphuysen 1999), limiting possibilities to observe foraging behaviour from the shore during migration. Knowledge about foraging of Pomarine Skuas at sea is low (Furness 1987b) and restricted to anecdotal records (summarised in Glutz von Blotzheim & Bauer 1982). In summer 2000, the unusual occurrence of a

group of moulting immatures at the offshore island Helgoland (North Sea) gave opportunities to study kleptoparasitic behaviour of Pomarine Skuas.

METHODS

From early July to mid September 2000, we observed hunting behaviour of Pomarine and Arctic Skuas from the beaches of the offshore island Helgoland in the southeastern North Sea (54° 11' N, 07° 55' E). For any kleptoparasitic encounter we recorded species and age of the victim and all members of the hunting group. The outcome of an encounter was rated as successful when the attacked bird disgorged or dropped prey, irrespective of the success of any member of the hunting group to obtain it. Rapid flights of a skua towards another bird were not treated as an attack if the skua gave up clearly before any possible physical contact. Foraging modes other than kleptoparasitism were recorded anecdotally. Counts of Pomarine Skuas were obtained from the ornithological log of the Institut für Vogelforschung (1975-2000) and from the Ornithologische Arbeitsgemeinschaft Helgoland (1990-2000).

RESULTS

Unusual summer occurrence in 2000 On Helgoland, Pomarine Skuas are very rare spring migrants, but they regularly occur in small numbers during autumn migration from late July to October (Fig. 1). The influx of Pomarine Skuas observed along the European coastline between Sweden and Portugal in autumn 1999 (van den Berg 1999) was not noticed at Helgoland (Fig. 2). Apart from some migrants, two immature Pomarine Skuas (second and third calendar-year, respectively) were present at Helgoland from late May 2000 onwards, and were joined by a growing number of conspecifics in the second half of June (Fig. 1). The unusual summer occurrence peaked on 14 July with 16 birds, of which only one was adult (11 in second calendar-year, 4 in third calendar-year). Numbers remained high until mid August, but varying percentages of age classes suggest some degree of individual turnover. The number of adults never exceeded two. The assemblage of Pomarine Skuas decreased to six birds in the second half of August and disappeared in the first half of September. From June to August, several birds were moulting primaries, tail feathers and wing coverts, creating a very ragged appearance.

Foraging behaviour From June to early August, most Pomarine Skuas rested on the beach, from where they occasionally started their hunting excursions. In the second half of August and in September, the flock of resting birds remained mostly on the sea. During foraging, Pomarine Skuas were seen to patrol along

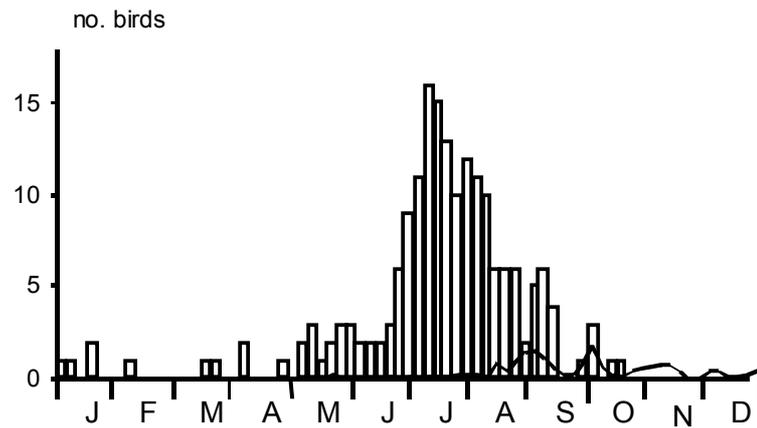


Figure 1. Occurrence of Pomarine Skuas on Helgoland in 2000 (maximum counts per five-day-period, $n = 187$; columns) and in 1995-1999 (average no. of birds per day, $n = 444$; continuous line).

Figuur 1. Voorkomen van Middelste Jagers rond Helgoland in 2000. Maximum aantal per vijfdaagse periode ($n = 187$; staafdiagram) en het gemiddelde aantal per dag gedurende 1995-1999 ($n = 444$; ononderbroken lijn).

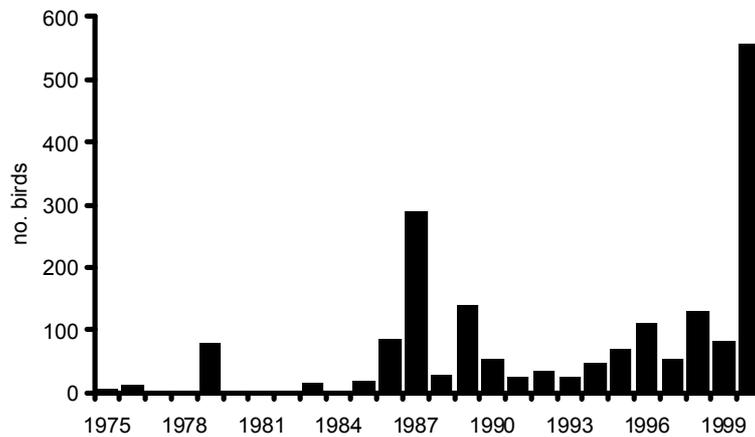


Figure 2. Annual totals of Pomarine Skuas observed on Helgoland. Individuals present for more than one day are considered for each day recorded.

Figuur 2. Aantal rond Helgoland waargenomen Middelste Jagers. Pleisterende exemplaren werden elke dag van hun aanwezigheid meegeteld.

Table 1. Species attacked by Pomarine and Arctic Skuas and success of attacks from July to September 2000. Species attacked while swimming or sitting on the beach are marked with asterisks.

Tabel 1. Door Middelste en Kleine Jagers aangevallen vogelsoorten tussen juli en september 2000. Soorten die werden aangevallen, terwijl zij in zee zwommen of op het strand stonden, zijn met een asterisk gemerkt.

Aggressor	Pomarine Skua			Arctic Skua			
	n	success	%	n	success	%	
Host		yes	no		yes	no	%
Northern Gannet <i>Monus bassanus</i>	3	0	3	1	0	1	
Great Cormorant <i>Phalacrocorax carbo</i> *	1	0	1	1	0	1	
Mallard <i>Anas platyrhynchos</i> *	1	0	1				
Common Eider <i>Somateria mollissima</i> *	6	0	6				
Common Scoter <i>Melanitta nigra</i> *	1	0	1				
Red-breasted Merganser <i>Mergus serrator</i> *	1	0	1				
Honeybuzzard <i>Pernis apivorus</i>	2	0	2				
Oystercatcher <i>Haematopus ostralegus</i> *	6	0	6				
Golden Plover <i>Pluvialis apricaria</i> *	1	0	1				
Sanderling <i>Calidris alba</i> *	1	0	1	1	0	1	
Redshank <i>Tringa totanus</i> *	2	0	2				
Greenshank <i>T. nebularia</i> *	3	0	3				
Turnstone <i>Arenaria interpres</i> *	1	0	1				
Pomarine Skua <i>Stercorarius pomarinus</i>	3	0	3				
Black-headed Gull <i>Larus ridibundus</i>	4	0	4	1	0	1	
Common Gull <i>L. canus</i>	2	0	2	1	0	1	
Herring Gull <i>L. argentatus</i>	7	0	7				
Great Black-backed Gull <i>L. marinus</i>	4	0	4	2	0	2	
Black-legged Kittiwake <i>Rissa tridactyla</i>	208	63	145	30	22	4	18
Common/Arctic Tern <i>Sterna hirundo/paradisaea</i>	5	1	4	7	3	4	
Sandwich Tern <i>S. sandvicensis</i>	29	3	26	10	13	2	11
Carrion Crow <i>Corvus corone</i>	2	0	2				

the stretch of sea 0.5-5 km from the seabird colony, mainly in the west to north sector. However, arrivals from nearly all destinations indicate that hunting excursions were directed to other areas as well. All species attacked are listed in Table 1. Most victims were Black-legged Kittiwakes *Rissa tridactyla*, the most abundant breeding species on Helgoland (7968 occupied nests in 2000). Attacks were only directed against Black-legged Kittiwakes approaching the colony, while birds flying towards the sea were ignored. The only other seabirds frequently attacked were Sandwich Terns *Sterna sandvicensis*, which do not breed at Helgoland, although several hundred migrants or non-breeders were present throughout the summer. Whereas gulls and terns were always attacked in flight, chases against ducks were directed against swimming birds. Waders were attacked either on the ground or chased in flights close to the beach surface. On several occasions it was noted that Pomarine Skuas swallowed

Table 2. Composition of hunting groups in attacks against Black-legged Kittiwakes on Helgoland from July to September 2000.

Tabel 2. Samenstelling van jagende groepen bij aanvallen op Drieteenmeeuwen op Helgoland, juli-september 2000.

Number of birds in attack group					n	Success	
Pomarine Skua	Arctic Skua	Herring Gull	Lesser Bl backed Gull	Great Black-backed Gull		yes	no
1	-	-	-	-	160	45	115
2	-	-	-	-	16	7	9
3	-	-	-	-	5	0	5
4	-	-	-	-	1	0	1
5	-	-	-	-	1	1	0
1	1	-	-	-	2	0	2
1	-	-	1	-	1	1	0
1	-	1	-	-	13	7	6
1	-	-	-	1	1	0	1
1	-	1	1	-	1	0	1
1	-	2	-	-	2	0	2
1	-	3	-	-	1	0	1
2	-	1	-	-	2	1	1
2	-	-	-	1	1	1	0
3	-	1	-	-	1	0	1
5	-	1	-	1	1	1	0

pieces of kelp *Laminaria* spp. which they took from the shoreline. On 31 July, a flock of seven Pomarine Skuas was foraging much in the manner of Little Gulls *Larus minutus* by taking prey from the water surface.

A freshly disgorged pellet found on 14 July contained mainly vertebrae of Ammodytidae and Clupeidae, the main diet of Black-legged Kittiwake chicks on Helgoland in 2000 (A.-K. Dierschke pers. comm.). The pellet also contained otoliths of Sprat *Sprattus sprattus*, remnants of Blue Mussel *Mytilus edulis* shells and two spikes of sea urchins.

Hunting success Success rate of chases by Pomarine Skuas was 30% with Black-legged Kittiwakes, but significantly lower with Sandwich Terns (10%; $\chi^2 = 5.04$; $P = 0.025$). Compared to Pomarine Skuas, Arctic Skuas were more successful with Sandwich Terns (18%) and less successful with Black-legged Kittiwakes (22%), but differences were not significant between skua species (Black-legged Kittiwake $\chi^2 = 1.41$, $P = 0.235$; Sandwich Tern Fisher's exact test $P = 0.637$). Arctic Skua success rates did not differ between Black-legged Kittiwakes and Sandwich Terns (Fisher's exact test $P = 1.000$). The high success of Arctic Skuas chasing Arctic/Common Terns *Sterna paradisaea/hirundo* (3 out of 7 against 1 out of 5, Table 1) further indicates that Arctic Skuas do better chasing smaller host species than Pomarine Skuas.

Immature Pomarine Skua, note the ragged appearance Onvolwassen Middelste Jager met sterk gesleten kleed (J.-P. Daniels)

When looking on attacks of single hunting Pomarine Skuas on Black-legged Kittiwakes only, age did not seem to affect the rate of success. Birds in second calendar-year (28%) were only slightly less successful than birds in third calendar-year (34%; $\chi^2 = 0.56$, $P = 0.456$).

The number of birds involved in an attack did not much influence the outcome, as groups of Pomarine Skuas were only slightly more successful (35%) than single birds (28%; $\chi^2 = 0.43$, $P = 0.510$) against Black-legged Kittiwakes. Slightly more successful than groups of Pomarine Skuas (35%) were mixed-species groups (42%; $\chi^2 = 0.24$, $P = 0.627$), in which Pomarine Skuas were joined by gulls and Arctic Skuas (Table 2). Attacks of mixed-species groups were always initiated by a Pomarine Skua. The success per group member declined from 0.28 prey/attack in single Pomarine Skuas ($n = 160$) to 0.23 in groups of two birds (including gulls, $n = 32$), 0.03 in three birds ($n = 11$) and 0.08 in 4-7 birds ($n = 5$). When hunting in mixed groups, prey was secured by Herring Gulls *Larus argentatus* in five incidents, obtained by Pomarine Skuas in two incidents and shared between both species in another two incidents. If multiple chasing was a result of a short come of host birds, then

group hunting might increase towards the end of the breeding season of Black-legged Kittiwakes if there are decreasing numbers of food-carrying birds flying to the colony (Furness 1978). This could not be proven, as group hunting tended to be more common in July (25% of all attacks against Black-legged Kittiwakes, $n = 157$) than in August (15%, $n = 46$; $\chi^2 = 1.88$, $P = 0.170$), but note that the number of Pomarine Skuas was already lower in August (Fig. 1).

DISCUSSION

During the breeding season, the many thousand of adult seabirds carrying food to their offspring in the Helgoland colony can be regarded as a rewarding foraging opportunity for skuas, which specialised in kleptoparasitism of seabirds. But although occurring in tens or even hundreds of individuals per day during autumn migration, skuas are scarce from May to August. The presence of a group of Pomarine Skuas in summer 2000 indicates that a number of skuas is able to exist around Helgoland, but in almost all years this large food resource is not used and thus appears to be under-exploited. Such a situation was also found in the western Mediterranean Sea, where only few skuas occur despite high numbers of gulls and terns as potential hosts (Paterson 1986). That conditions at Helgoland are suitable for skuas is also indicated by success rates in kleptoparasitism which are similar to those of non-breeding Arctic Skuas observed in the Mediterranean Sea (Paterson 1986, Arcos 2000) and off South Africa (Furness 1983).

The high number of Pomarine Skuas present at Helgoland in summer 2000 is surprising as this species is usually rare in summer in the North Sea according to both ship- and land-based counts (Fig. 3, Camphuysen 1999). Immature non-breeders are thought to remain at sea in the North Pacific and North Atlantic in summer, but also visit the Arctic breeding grounds (Furness 1987a, Malling Olsen & Larsson 1997). Perhaps the high numbers in summer 2000 are connected with the influx of Pomarine Skuas to northern and western Europe in autumn 1999 (Van den Berg 1999), which might also be responsible for a number of records at Helgoland in late autumn 1999 and winter 1999/2000 (see above). At Helgoland, summer occurrences of Pomarine Skuas were observed before only twice. In 1979, an adult and an immature bird were present on the beach from late June throughout July (Kuschert 1981). In 1987, up to 31 birds were counted between early August and mid September, but with much higher turnover of individuals and less bond with the beach (V.D. and F. Stühmer pers. obs.).

In this study, Pomarine Skuas mainly attacked Black-legged Kittiwakes, the most abundant seabird species around Helgoland in summer. As

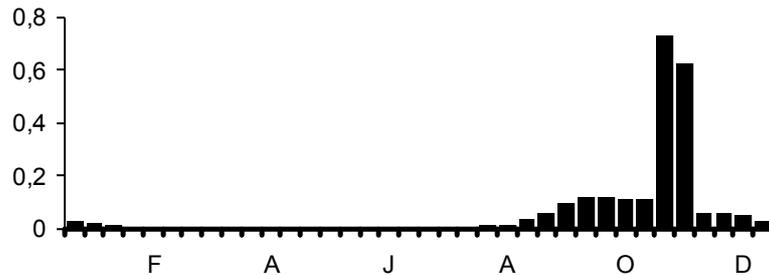


Figure 3. Pomarine Skuas per hour per 10-day period, based on seawatches along the Dutch coast 1972-2000 (n = 76191 hours of observation, 5551 Pomarine Skuas observed, source CvZ/NZG, unpubl. data).

Figuur 3. Middelste Jagers per uur per 10-daagse periode, op basis van zeezichtingen aan de Nederlandse kust, 1972-2000 (n = 76191 waarnemingsuren, 5551 Middelste Jagers, CvZ/NZG ongepubl. materiaal).

the expectation of success was found to correlate with the selection of host species in studies on Arctic Skuas (Taylor 1979, Arcos 2000), another reason to attack Black-legged Kittiwakes probably is the higher rate of success compared to Sandwich Terns, which should be suitable hosts because of their very accessible way to carry fish in the bill. However, manoeuvrability is less developed in Pomarine than in Arctic Skuas and might therefore limit the exploitation of the more agile terns. Therefore, with respect to the best fitting host species, Pomarine Skuas are placed between Arctic Skuas (which in other studies often or even exclusively attack terns; Taylor 1979, B elisle 1998, Arcos 2000) and Great Skuas (which are unable to kleptoparasitise terns and attack Black-legged Kittiwakes less than Arctic Skuas do; Furness 1978). Because the Pomarine Skuas observed in this study were moulting part of their flight feathers, it is possible that their manoeuvrability was reduced and perhaps the selection of hosts species was shifted in favour of Black-legged Kittiwakes rather than terns.

Group hunting of Pomarine Skuas did not increase the success rate per host attacked. This is in line with Arctic Skuas during spring migration in the Mediterranean Sea (Arcos 2000), but in contrast to Arctic Skuas during migration in Scotland (Taylor 1979) and eastern Canada (B elisle 1998). However, as in Arctic Skuas during breeding in Iceland (Amason & Grant 1978), the success of an individual group member decreased with increase of the number of individuals involved in a hunting event.

Age differences in the success rate of Arctic Skuas were reported in the Mediterranean Sea in the non-breeding season (Paterson 1986), but the author only grouped birds into adults and "juveniles". In this study, it was possible to compare birds in second and third calendar-year, but no difference in success rate was found when attacking Black-legged Kittiwakes. Perhaps experience is not a crucial factor anymore when a Pomarine Skua is already one year old, but larger sample sizes are required to allow a more detailed analysis.

Occasionally, Pomarine Skuas were observed foraging other than attacking seabirds. Hunting waders at or close to the beach might compare to predation on small seabirds and phalaropes which is thought to be an important mode of feeding for Pomarine Skuas wintering off West Africa (Furness 1987a). It remains unclear for what reason Pomarine Skuas ingested pieces of kelp. Perhaps this is related to the intake of carrion as reported from the shoreline of the German North Sea coast (Gloe 1987).

ACKNOWLEDGEMENTS

We are thankful for comments on the manuscript from Franz Bairlein, Kees Camphuysen, Stefan Garthe, Ommo Hüppop and two anonymous referees.

FOERAGEGEDRAG VAN NIET-BROEDENDE MIDDELSTE JAGERS *STERCORARIUS POMARINUS* IN DE NOORDZEE IN DE ZOMER

Van eind mei tot half september 2000 verzamelden zich ongewoon veel Middelste Jagers *Stercorarius pomarinus* in de Duitse Bocht rond het eiland Helgoland. De meeste van de maximaal 16 exemplaren waren onvolwassen (2^e en 3^e kalenderjaar) en zij vertoonden rui van de slagpennen, staartveren en bovenvleugeldekenen. De jagers leefden vooral van het voedsel dat door Drieteenmeeuwen *Rissa tridactyla* in de broedkolonie werd aangevoerd (kleptoparasitisme). Het succes van hun aanvallen was bij Drieteenmeeuwen aanmerkelijk hoger dan bij de andere vogels die werden belaagd (bijv. Grote Stem *Stema sandvicensis*, noordse/dief *S. paradisaea/hirundo*). Daarmee zou de Middelste Jager gerangschikt kunnen worden tussen de Kleine Jager *S. parasiticus* (die vooral stems bejaagd) en de Grote Jager *S. [Catharacta] skua* (weinig succesvol bij stems, minder vaak Drieteenmeeuwen aanvallend dan de kleinere jagersoorten). Bij de jacht op Drieteenmeeuwen hadden de leeftijd van de jagers, noch de grootte van de aanvallende groep (waarin soms ook Zilvermeeuwen participeerden) invloed op het succespercentage. In grotere groepen nam het individuele foerageersucces echter aanmerkelijk af. Het ongebruikelijke, maar kennelijk succesvolle voorkomen van een ruiende groep Middelste Jagers in de zomer in de zuidelijke Noordzee suggereert dat de Duitse Bocht voor deze soort een geschikt overzomeringsgebied zou kunnen vormen.

REFERENCES

- Arcos J.M. 2000. Host selection by Arctic Skuas *Stercorarius parasiticus* in the North-western Mediterranean during spring migration. *Omis Fennica* 77: 131-135.
- Arnason E. & Grant P.R. 1978. The significance of kleptoparasitism during the breeding season in a colony of Arctic Skuas *Stercorarius parasiticus* in Iceland. *Ibis* 120: 38-54.
- Bélisle M. 1998. Foraging group size: models and a test with jaegers kleptoparasitizing terns. *Ecology* 79: 1922-1938.

- Van den Berg A.B. 1999. WP reports. Dutch Birding 21: 351-359.
- Camphuysen C.J. 1999. Jagers in de Nederlandse kustwateren. Graspieper 19: 53-65.
- Furness B.L. 1983. The feeding behaviour of Arctic Skuas *Stercorarius parasiticus* wintering off South Africa. Ibis 125: 245-251.
- Furness R.W. 1978. Kleptoparasitism by great skuas (*Catharacta skua* Brünn.) and arctic skuas (*Stercorarius parasiticus* L.) at a Shetland seabird colony. Anim. Behav. 26: 1167-1177.
- Furness R.W. 1987a. The skuas. T & AD Poyser, Calton.
- Furness R.W. 1987b. Kleptoparasitism in seabirds. In: Croxall J.P. (ed) Seabirds: feeding ecology and role in marine ecosystems: 77-100. Cambridge Univ. Press, Cambridge.
- Gloe P. 1987. Raubmöwen (*Stercorariidae*) im zweiten Halbjahr 1985 in Schleswig-Holstein und Hamburg. Corax 12: 94-122.
- Glutz von Blotzheim U.N. & Bauer K.M. 1982. Handbuch der Vögel Mitteleuropas. Band. 8. Akademische Verlagsgesellschaft, Frankfurt a. M.
- Kuschert H. 1981. Das Vorkommen der Raubmöwen (*Stercorariidae*) auf Helgoland unter besonderer Berücksichtigung des Einfluges im Sommer 1979. Vogelwelt 102: 121-132.
- Malling Olsen K. & Larsson H. 1997. Skuas and jaegers. A Guide to the Skuas and Jaegers of the World. Pica Press, Sussex.
- Meltofte H. 1979. Forekomsten af kjoever *Stercorarinae* ved Blåvandshuk 1963-1977. Dansk. Om. Foren. Tidsskr. 73: 297-304.
- Paterson A.M. 1986. Kleptoparasitic feeding by migrating skuas in Malaga Bay, Spain. Ringing & Migration 7: 51-55.
- Platteeuw M., van der Ham N.F. & den Ouden J.E. 1994. Zeetrektingen in Nederland in de jaren tachtig. Sula 8: 1-203.
- Taylor I.R. 1979. The kleptoparasitic behaviour of the Arctic Skua *Stercorarius parasiticus* with three species of tern. Ibis 121: 274-282.

THE TIME OF FIRST RETURNS TO LAND BY
CORY'S SHEARWATER *CALONECTRIS*
[*DIOMEDEA*] *BOREALIS*¹ ON SELVAGEM GRANDE
DURING THE BREEDING PERIOD

J.-L. MOUGIN, Chr. JOUANIN & F. ROUX

Mougin J.-L., Jouanin Chr. & Roux F. 2002. The time of first returns to land by Cory's Shearwater *Calonectris [diomedea] borealis* on Selvagem Grande during the breeding period. *Atlantic Seabirds* 4(2): 63-72. *The time of first returns to land within each attendance cycle by Cory's Shearwater Calonectris [diomedea] borealis on Selvagem Grande (30°09'N, 15°52'W) is negatively correlated with the number of birds that will come to land in the evening. However, the mean time of first returns for each attendance cycle shows no significant variation from May to September. The Cory's Shearwaters of Selvagem Grande are partly diurnal for at least part of their breeding cycle, in contrast to their conspecifics at other Mediterranean and Atlantic breeding localities. This behaviour may originate from when the size of the breeding population was very large, before its overexploitation and depredations in the 1960s and 1970s, and also linked to the lack of diurnal predators.*

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INTRODUCTION

Of the 60 or so acknowledged species of Procellariids, only about one tenth are diurnal. Cory's Shearwaters *Calonectris diomedea*² are usually nocturnal, and during the breeding season come to land after sunset to display at almost all the breeding localities in the Mediterranean and Atlantic (Bannerman 1914; Lockley 1952; Mallett & Coghlan 1964; Winthrop 1973; Servent 1987). The population of Selvagem Grande (30°09'N, 15°52'W), the largest of the Portuguese Selvagens Islands, situated between Madeira and the Canary Islands, is atypical in that its activities are partly diurnal, the first returns to land of the birds occurring before sunset during some summer weeks.

Having spent the boreal winter in the southern hemisphere, Cory's Shearwaters return to Selvagem Grande, as well as the other breeding localities, at the end of February and beginning of March. Eggs are laid at the end of May/beginning of June and, on average 54 days later, hatch during the second fortnight of July. Chicks, no longer brooded after a few days, are left alone in the nesting burrow; their period of growth is about 95 days. The fledglings leave the colony with the adults at the end of October and beginning of November (Zino 1971; Zino *et al.* 1987).

Table 1. Parameter estimates of the multiple regression model used to assess the contribution of bird numbers, date and sunset time in explaining the time of the first returns to land of Cory's Shearwaters on Selvagem Grande.

Tabel 1. Parameters van het multiple regressiemodel dat gebruikt werd om de invloed te schatten van aantallen, datum en het tijdstip van zonsondergang bij het verklaren van het tijdstip van terugkeer van Kuhls Pijlstormvogels op Selvagem Grande.

Variables	Coefficient	<i>t</i>	<i>P</i>
Numbers	-1.252	-8.03	0.000
Date	0.141	0.89	0.379
Sunset time	-0.025	-0.09	0.932

Visits made by the adults to the colonies of Selvagem Grande - both sexes together during the pre-egg period but separately during incubation and chick rearing - show daily variations in both the number of birds and the time of the first returns; the number of visiting birds varies regularly between a minimum and a maximum according to a sinusoid, the half-period of which is 5 days (Jouanin *et al.* 1989; Mougin *et al.* 2000). In this paper, we attempt to discover precisely the time of the first returns during the whole breeding period and the factors that influence it.

METHODS

Data on the time of return to land of the birds of Selvagem Grande were collected in a subcolony of about 100 pairs during three 3-week visits (May 1991, June-July 1988, September 1993). Birds present on land were counted daily at intervals of 15 mins. between the first and the last return. A torch was used when necessary. Casual observations made in June and July in previous years showed no important differences from the 1988 data, so we feel confident that the use of data spread over three years might allow seasonal comparisons.

We used multiple regression to assess the contribution of various factors in explaining variation in the time of the first returns to land, chi-square to test the differences in the distribution of returns relative to sunset during the three periods studied, Pearson's correlation to investigate the relationship between the number of birds coming ashore and the time of the first returns, and analysis of variance to compare the average number of birds coming ashore per unit time during the three periods studied. Means are presented \pm SD.

RESULTS

Factors influencing the time of the first returns A multiple regression with the time of first returns as dependent variable and date, numbers of birds and

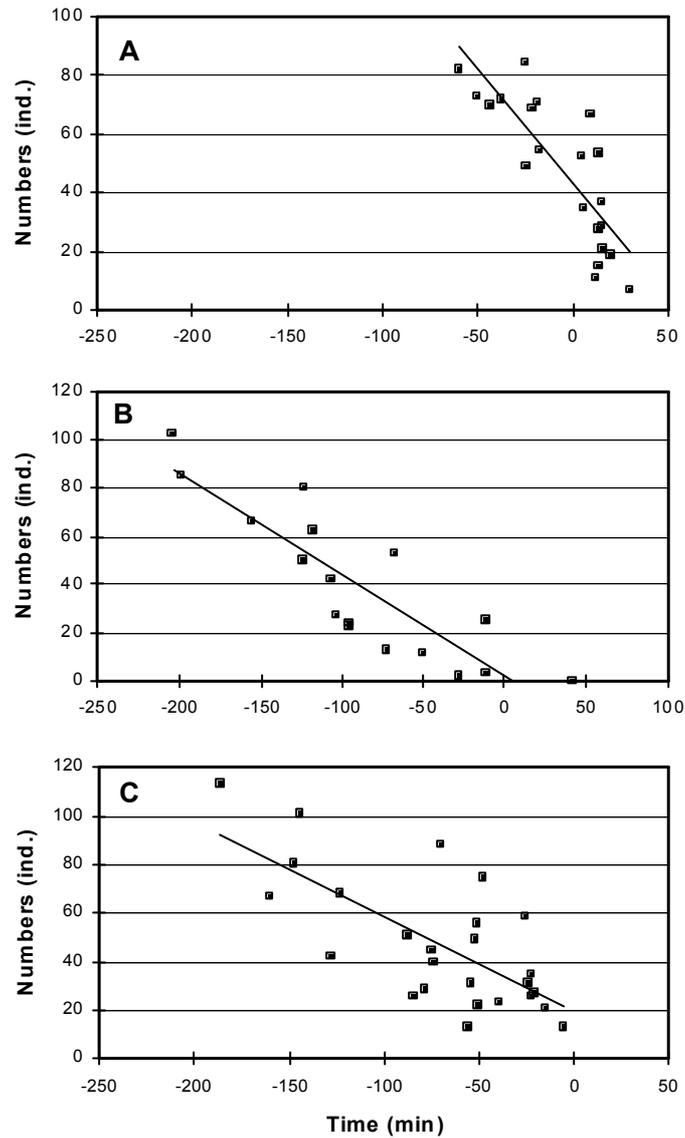
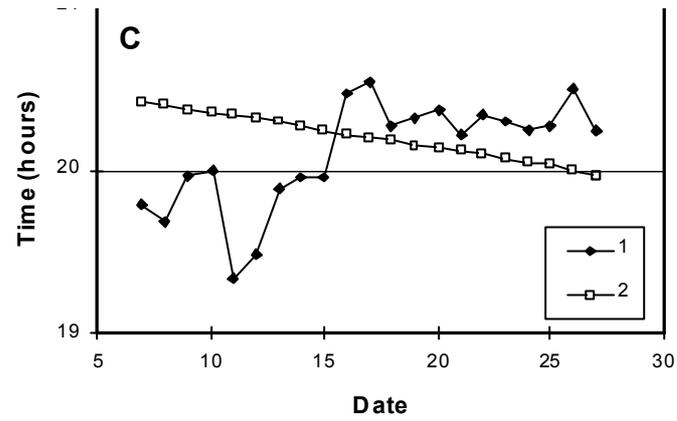
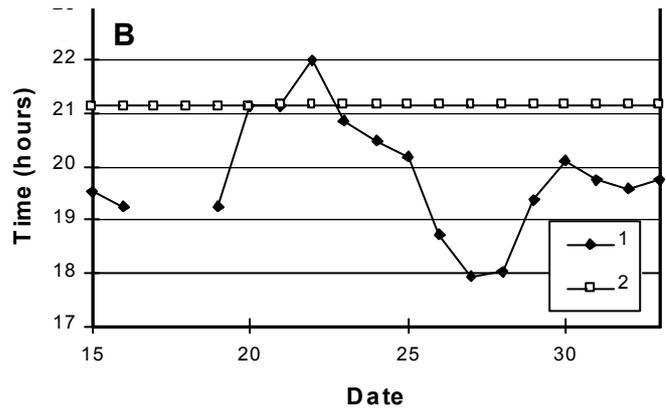
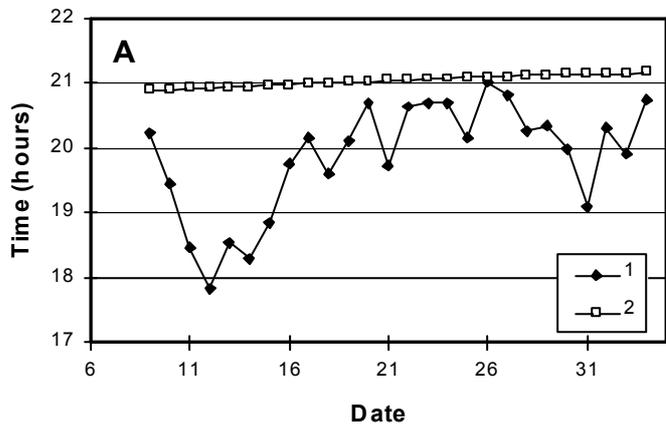


Figure 1. Time of the first returns to the colonies as a function of the number of birds present. A: May; B: June-July; C: September. 0 = sunset time.

Figuur 1. Tijdstip van terugkeer in de kolonie als functie van het totaal aantal arriverende vogels. A: mei; B: juni-juli; C: september. 0 = zonsondergang.



Opposite page: Figure 2. Time of the first returns to the colonies as a function of date and sunset time. 1: time of the first returns; 2: sunset time. A: May; B: June-July; C: September. The time between 17 and 27 May corresponds approximately to the pre-laying exodus.

Tegenoverliggende pagina: Figuur 2. Tijdstip van terugkeer in de kolonie als functie van datum en het tijdstip van zonsondergang. 1: tijdstip van terugkeer, 2: zonsondergang, A: mei; B: juni-juli; C: september. De periode van 17-27 mei valt ongeveer samen met de 'pre-laying' exodus van Kuhls Pijlstormvogels.

sunset time as independent variables revealed that only bird numbers were important, explaining 50.5% of the variation in the dependent variable (Table 1). Figure 1 shows a significant correlation between numbers and time of first returns during the three periods studied (respectively $r_{26} = -0.687$, $P < 0.001$ for May, $r_{17} = -0.873$, $P < 0.001$ for June-July and $r_{21} = -0.759$, $P < 0.001$ for September).

No correlation exists between the time of first returns and date ($r_{64} = 0.169$, n.s.). The average time of the first returns was $19.54 \text{ hr} \pm 48 \text{ min}$ ($n = 64$), the range of variation between earliest and latest first returns being particularly large in June-July. The average interval between first returns to land and sunset varied between May and September (Fig. 2). During the pre-laying exodus, the exceptional scarcity of the birds was associated with unusually late first returns - only $43 \pm 25 \text{ min}$ ($n = 10$) before sunset. With this exception, the first returns until July occurred on average $85 \pm 61 \text{ min}$ ($n = 32$) before sunset, with large daily variations (coefficient of variation: 71.8%). From July onwards, the interval steadily decreased. During the second week of September, the first returns were observed $25 \pm 23 \text{ min}$ ($n = 9$) before sunset, but $12 \pm 5 \text{ min}$ ($n = 12$) after sunset during the third and fourth weeks. The first returns, which always occurred before sunset at the end of the pre-egg stage and during incubation and the beginning of chick rearing, were therefore observed after sunset during the last weeks of chick rearing.

Timing of returns Figure 3, based on counts performed at 15 min intervals, shows monthly differences not so much in the time elapsed between the first and last return and thus in the average rate of returns ($F_{2, 35} = 0.64$, n.s.) but in the distribution of returns relative to sunset time ($\chi^2 \geq 36.6$, $n \geq 14$, $P < 0.01$). The birds returned to their colonies regularly and slowly in June-July, mostly before sunset (21.18 hr on average). In May, they lingered at sea long after the return of their earliest conspecifics before returning slowly, mostly after sunset (21.04 hr), the last birds being particularly aggregated. Lastly, in September, the returning birds were grouped after sunset (20.12 hr), the earliest birds returning swiftly and the later ones much more slowly, the reverse of the pattern in May.

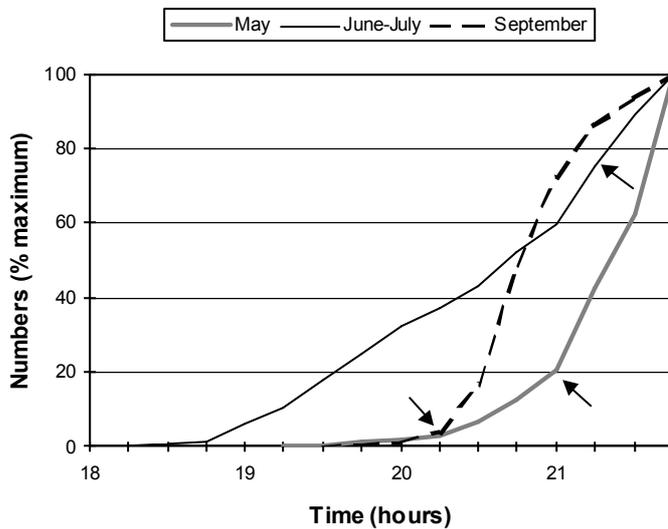


Figure 3. Timing of the returns to the colonies as a function of date. The arrows indicate the time of sunset.

Figuur 3. Tijdstip van terugkeer in de kolonie als functie van de datum. De pijlen laten het tijdstip van zonsondergang zien.

Thus, 65.8% of the birds returned to their colonies before sunset in June-July, 13.2% in May and 3.8% in September ($\chi^2_2 = 1180.2$, $P < 0.01$). In fact, 6.6% returned before sunset by mid September and none after this.

DISCUSSION

The reasons that there exists a strong relationship between the numbers of arriving birds and the time of first arrivals on Selvagem Grande, in contrast to other Cory's Shearwater colonies, are not clear. Nor is it known why, during some summer weeks, the first arrivals (but never all of them) are diurnal on Selvagem Grande but are not diurnal elsewhere (Hartert & Ogilvie Grant 1905; Bannerman 1914; Lockley 1952; Mallett & Coghlan 1964; Fernandez 1979; Thibault 1985; Martin *et al.* 1991).

Various hypotheses have been suggested to account for the birds' diurnal habits including habitat structure, availability of prey and predator avoidance (Granadeiro *et al.* 1998; Klomp & Furness 1992). Even if a disturbed

habitat is likely to discourage nocturnal behaviour, many birds are in fact nocturnal on Selvagem Grande and besides, the habitat here is relatively undisturbed. Similarly, the availability of prey is the same for the partly diurnal birds of the Selvagens and for their nocturnal conspecifics of the Canary Islands, which prospect the same waters of the Canary Current (Mougin & Jouanin 1997). Two species have been reported to prey upon Cory's Shearwaters - humans and the Yellow-legged Gull *Larus cachinnans*³. However, the Yellow-legged Gull is not a predator of Cory's Shearwaters on Selvagem Grande, even less of adults than of eggs and chicks; the large body size of the shearwater protects it from the gull. Past predation by humans on Cory's Shearwaters was mostly on chicks and occurred at the end of September and beginning of October during the morning hours when adults were not present in the colonies (Schmitz 1893); similar exploitation occurred in the Canary Islands (Lovegrove 1971; Martin *et al.* 1991). It is unlikely that a nocturnal species would become diurnal to avoid diurnal predators. Thus, the various hypotheses do not accord well with our observations. We propose as an alternative hypothesis that the observed diurnal behaviour is a consequence of very high breeding numbers.

Today, the size of the breeding population of Selvagem Grande, about 36 000 birds (Mougin *et al.* 1996), is very much reduced following exploitation and poaching. At one time, the population numbered about 300 000 birds, 250 000 of which probably landed to prospect or breed. All of these would congregate on an area of about 2 km². It seems unlikely that so many birds could have displayed in flight in close proximity and in the dark without collisions, and in the absence of conditions conducive to good transmission of the information conveyed by their songs. Population pressure may thus have resulted in a switch to diurnal activity, rendered possible by the lack of predators. Such a shift to diurnal behaviour has been observed in superabundant populations of another large shearwater, the Sooty Shearwater *Puffinus griseus* in New Zealand (Serventy *et al.* 1971), but not in abundant populations of smaller shearwaters liable to predation such as the Manx Shearwater *Puffinus puffinus*, for example (Brooke 1990).

Clearly, the almost complete absence of predators could have permitted partly diurnal habits in many other localities, but populations of Cory's Shearwater may never have been large enough to effect a shift - 45 000-50 000 breeding pairs when numbers were at their peak on the 10.5 km² of Aleganza, Canary Islands (Martin *et al.* 1991; Martin & Nogales 1993) and 20 000-25 000 pairs on the 3.4 km² of Zembra (Gaultier 1981), both localities being known to host the most abundant populations of Cory's Shearwater after Selvagem Grande.

Cory's Shearwater on Selvagem grande Kuhls pijlstormvogel op Selvagem grande
(J.-L. Mougin)

The decline in numbers during the last few decades has not resulted in a reversion to strictly nocturnal behaviour in the birds of Selvagem Grande. In fact, the partly diurnal behaviour they exhibit is by no means disadvantageous and there has been no pressure for change. Besides, the population decline has been very sharp and is a relatively recent phenomenon.

The relationship between bird numbers and time of first returns observed on Selvagem Grande might have been expected; the larger the sample size then the wider the range and the earlier the first record - the birds perhaps acquiring information on the number of conspecifics expected to be in the colonies that night in the rafts where they settle during the afternoon, sometimes for hours, before returning to their colonies. However simple and obvious such a relationship may be, it has not been observed in the other breeding localities insofar as one can judge by the data published (Bannerman 1914; Mallett & Coghlan 1964; Fernandez 1979; Vaughan 1980; Servent 1987); the first returns usually occur at fairly constant times except during moonlit nights (Klomp & Furness 1992). This being so, either the numbers are constant day after day,

which would imply the absence of the attendance cycles observed on Selvagem Grande, or attendance cycles exist but have no influence on the hours of first returns. Data on the overall numbers of Cory's Shearwaters present nightly would resolve the problem but are at present lacking.

ACKNOWLEDGEMENTS

We thank Henrique Costa Neves, director of the Parque Natural da Madeira, for giving us the necessary authorisation to stay in the Nature Reserve of the Selvagens Islands, and the captains of NRP for providing our transport to and from Madeira-Selvagens. We are grateful to Manuel José Biscoito, director of the Museu Municipal do Funchal and President of the Comissão Instaladora do Parque Natural da Madeira, for his constant support. We also thank the rangers of the Reserve for their daily help and Pierre Defos du Rau for his excellent assistance in the field in 1993. We wish to acknowledge Paul Alexander Zino, Francis Zino, Mrs Yvonne Zino and Mrs Elizabeth Zino for their friendly help and always warm hospitality in Madeira. Many thanks to Hugh Davenport who helped with the English.

HET TIJDSTIP VAN AAN LAND KOMEN DOOR KUHLS PIJLSTORMVOGELS *CALONECTRIS [DIOMEDEA] BOREALIS*¹ OP SELVAGEM GRANDE IN DE BROEDTIJD

Het tijdstip van het aan land komen door Kuhls Pijlstormvogels Calonectris [diomedea] borealis¹ op Selvagem Grande (30°09'N, 15°52'W) blijkt negatief gecorreleerd te zijn met het aantal vogels dat per avond naar de kolonie terugkeert. De gemiddelde aankomsttijd vertoont van mei tot september echter geen significante verschillen. In tegenstelling tot hun verwanten in andere Atlantische kolonies en in kolonies in de Middellandse Zee komen de Kuhls Pijlstormvogels van Selvagem Grande niet alleen 's nachts aan land. Dit gedrag kan nog stammen uit de tijd dat de kolonies op Selvagem Grande enorm groot waren, voordat de overexploitatie in de jaren zestig en zeventig haar tot had geëist. Populatie-druk kan hebben geleid tot dagactiviteit, hetgeen mogelijk was door een ontbreken aan predatoren gedurende de dag.

REFERENCES

- Bannerman D.A. 1914. An ornithological expedition to the eastern Canary Islands. *Ibis* 10: 38-90, 228-293.
- Brooke M. 1990. The Manx Shearwater. T & A. D. Poyser, London.
- Fernandez O. 1979. Observations sur le Puffin cendré *Calonectris diomedea* nicheur sur les îles marseillaises. *Alauda* 47: 65-72.
- Gaultier T. 1981. Contribution à l'étude de la population de Puffins cendrés (*Calonectris diomedea*) de l'île de Zembra (Tunisie). *Inst. Rech. Sc. Tech.*, Tunis.
- Granadeiro J.P., Burns M.D. & Furness R.W. 1998. Patterns of activity and burrow attendance in Cory's Shearwater *Calonectris diomedea* as revealed by a novel logging technique. *Ibis* 140: 458-466.
- Hartert E. & Ogilvie Grant W.R. 1905. On the birds of the Azores. *Nov. Zool.* 12: 80-128.
- Jouanin Chr., Roux F. & Mougin J.-L. 1989. Cycles d'affluence des Puffins cendrés (*Calonectris diomedea borealis*) à Selvagem Grande. *L'Oiseau et R.F.O.* 59: 153-168.
- Klomp N.I. & Furness R.W. 1992. Patterns of chick feeding in Cory's Shearwaters and the association with ambient light. *Colonial Waterbirds* 15: 95-102.
- Lockley R.M. 1952. Notes on the birds of the islands of the Berlengas (Portugal), the Desertas and Baixo (Madeira) and the Salvages. *Ibis* 94: 144-157.

- Lovegrove R. 1971. B.O.U. supported expedition to north-east Canary Islands. *Ibis* 113: 269-272.
- Mallett G.E. & Coghlan L.J. 1964. Cory's Shearwater *Procellaria diomedea* breeding on the Azores. *Ibis* 106: 123-125.
- Martin A. & Nogales M. 1993. Ornithological importance of the island of Alegranza (Canary Islands). *Bol. Mus. Mun. Funchal sup.* 2: 167-179.
- Martin A., Nogales M., Quilis V., Delgado G., Hernandez E. & Trujillo O. 1991. La colonie de Puffins cendrés (*Calonectris diomedea*) de l'île d'Alegranza (Lanzarote/iles Canaries). *Bol. Mus. Mun. Funchal* 43: 107-120.
- Mougin J.-L., Granadeiro J.P. & Oliveira P. 1996. L'évolution des effectifs des reproducteurs chez le Puffin cendré *Calonectris diomedea borealis* de Selvagem Grande (30°09'N, 15°52'W) de 1992 à 1995. *Bol. Mus. Mun. Funchal* 48: 171-178.
- Mougin J.-L. & Jouanin Chr. 1997. Prospection alimentaire du Puffin cendré *Calonectris diomedea borealis* de Selvagem Grande (30°09'N, 15°52'W) pendant l'incubation, par télémétrie satellitaire. *C.R. Acad. Sci. Paris* 320: 825-831.
- Mougin J.-L., Jouanin Chr. & Roux F. 2000. The attendance cycles of the Cory's Shearwater *Calonectris diomedea borealis* on Selvagem Grande. *C.R. Acad. Sci. Paris* 323: 385-390.
- Schmitz E. 1893. Die Puffin-jagd auf den Selvagens-Inseln im Jahre 1892. *Ornithologisches Jahrbuch* 4: 141-148.
- Servent A.G. 1987. La colonia de Pardela cenicienta mediterranea, *Calonectris diomedea* (Scopoli), de las islas Columbretes. In: Alonso Matilla L.A., Carretero J.L. & Garcia-Carrascosa A.M. (eds.) *Islas Columbretes, Contribución al estudio de su medio natural*: 223-240. Conselleria d'obres públiques, urbanisme i transports, Generalitat Valenciana, Valencia.
- Serventy D.L., Serventy V.N. & Warham J. 1971. *The Handbook of Australian Sea-birds*. A.H. & A.W. Reed, Sydney.
- Thibault J.-C. 1985. La reproduction du Puffin cendré *Calonectris diomedea* en Corse. In: *Oiseaux marins nicheurs du Midi et de la Corse*. *Ann. CROP* 2: 49-54.
- Vaughan R. 1980. Notes on Cory's Shearwater (*Calonectris diomedea*) and some other birds on Linosa, Pelagic Isles. *Riv. Ital. Orn.* 50: 143-154.
- Winthrop I. 1973. The Shearwaters of Diomedes. *Seabird Report* 3: 37-40.
- Zino P.A. 1971. The breeding of Cory's Shearwater *Calonectris diomedea* on the Salvage Islands. *Ibis* 113: 212-217.
- Zino P.A., Zino F., Maul T. & Biscoito J.M. 1987. The laying, incubation and fledging periods of Cory's Shearwaters *Calonectris diomedea borealis* on Selvagem Grande in 1984. *Ibis* 129: 393-398.

Footnotes

¹ *Calonectris diomedea borealis* is presently known as *Calonectris borealis* on the Dutch List (*Ardea* 87: 139-165).

² *Calonectris diomedea* was used as either the Mediterranean or the Atlantic race of Cory's Shearwater. On the Dutch list, these types are considered specifically distinct on the basis of phylogeographic analysis of allozymes and mitochondrial DNA, vocalisations and morphology (*Ardea* 87: 139-165) and the text should therefore read *Calonectris* sp.

³ *Larus cachinnans* is presently known as *Larus michahellis* on the Dutch List (*Ardea* 87: 139-165).

POMARINE SKUAS *STERCORARIUS POMARINUS* WINTERING OFF BRAZIL

FÁBIO OLMOS

Olmos F. 2002. Pomarine Skuas *Stercorarius pomarinus* wintering off Brazil. *Atlantic Seabirds* 4(2): 73-76. *In the Atlantic, Pomarine Skuas Stercorarius pomarinus have been rarely recorded in southern South America. At-sea observations made from bottom long-line fishing boats operating on the shelf off the Brazilian coast between 23°30'S and 29°S showed Pomarine Skuas to be present in March, May, October and November, but absent in July, and to be the commonest skua in the area. Most records were made in March, when up to 14 individuals were recorded at a time. Most birds seemed to be immatures. Pomarine Skuas are clearly more regular off Brazil than suggested by the current literature.*

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The Pomarine Skua *Stercorarius pomarinus* makes long annual migrations between its breeding areas in the Arctic and wintering grounds in the tropics and further south to southern Africa, Australia and New Zealand. Off southern South America, sparse available information suggested that Pomarine Skuas were vagrants (Furness 1987, Malling Olsen & Larsson 1997). There are few records of Pomarine Skuas in eastern South America south of the Caribbean. Escalante (1972, 1985) reported sight records for Punta del Este, Uruguay, and Cabo San Antonio, Argentina. The first Brazilian specimen, a female in second winter plumage, was collected at the mouth of the Tapajós River (around 03°30'S, 55°30'W) on 7 May 1960 (Escalante 1972). After that, Belton (1994) reported a sight record of a possible Pomarine Skua at 32°09'S, 50°09'W, and Olmos (1997) listed Pomarine Skuas among the seabirds attending bottom long-line fishing boats operating off Brazil between 25°15' and 27°49'S, but gave no details on skua records. Here further information is presented on records mentioned by Olmos (1997, 2000) and on new observations of Pomarine Skuas made off the southern Brazilian coast.

Data were collected during five cruises on board bottom long-line fishing vessels operating on the Brazilian shelf, mostly in waters less than 200 m deep. Shelf waters are strongly influenced by the warm, southward-flowing Brazil Current, but also by seasonal upwellings and the penetration of cold waters from the south in winter (Olmos 1997). Surface water temperature never dropped below 18°C during the observations, and was commonly around 22-26°C. Cruise dates were 23 - 27 Novembre 1994, 24 - 30 March 1995, 29 July - 7 August 1995, 3 - 9 Octobre 1996, and 26 May - 1 June 1997. The vessels

fished mainly near the shelf break and most skua observations were made on the shelf in waters less than 100 m deep. Bottom long-line fishing in Brazil has been described by Olmos (1997), Tutui *et al.* (2000) and Silva (2000). Seabird records were gathered by keeping a constant watch with the aid of binoculars during each day-time setting and hauling, recording the maximum number of birds of each species attending the boat (see Olmos 1997). So, the results provide the minimum number of individual birds present, as this method tends to underestimate the actual number of individuals due to turn-over of satiated birds and recruitment of new ones as the boat progress. Malling Olsen & Larsson's (1997) guide was used for the aging and identification of photographed specimens and assign them to age classes.

Pomarine Skuas were recorded during the November 1994, March 1995, October 1996 and May 1997 cruises, but were absent in July-August 1995 (Table 1). Pomarine Skuas were most frequent around the boats in March, when they were recorded almost every day. In fact, Pomarine Skuas made 15% of all bird records, only Spectacled Petrels *Procellaria conspicillata* being more abundant (58%). In March the skuas tended to stay in the same general area, with repeated sightings of the same recognizable individuals in consecutive days. Records made in May, October and November seem to refer to migrant birds only passing by and taking the opportunity for a snack. Skuas came quite close the fishing boat to feed, both by keeping on the wing and dipping for food and by sitting on the water waiting for discards to be thrown. Spectacled Petrels commonly supplanted skuas trying to get favored items like shark liver or whole bait (Argentine Squid *Ilex argentinus* and Chub Mackerel *Scomber japonicus*) discarded during hauling. The skuas fed mostly on floating scraps ignored by the petrels, like shark intestines and tilefish *Lopholatilus villarii* (Malacanthidae) viscera. Although skuas are considered surface feeders, some individuals sitting on the water would dive completely to at least 1 m deep to reach drifting discards passing below them; the clear water made it possible to see the skuas used their wings to dive, performing an underwater "somersault" before coming back to the surface. They would also probe kitchen discards thrown by the crew. No instance of predation on other birds was recorded but skuas would fight among themselves and try to kleptoparasitise each other. Unsuccessful attempts to steal food from Great Shearwaters *Puffinus gravis* (three) and Spectacled Petrels (four) were also observed in May. Great Shearwaters are aggressive enough to fight Yellow-nosed Albatrosses *Thalassarche chlororhynchos* trying to steal their food, and Pomarine Skuas were twice displaced from floating discards by Great Shearwaters. Spectacled Petrels did the same four times.

Table 1. Skua records off the Brazilian coast from bottom long-line fishing boats (individuals).
Tabel 1. Waargenomen jagers vanaf vissersschepen voor de kust van Brazilië (aantal individuen).

Date	Coordinates	<i>Stercorarius pomarinus</i>	<i>Stercorarius parasiticus</i>	<i>Stercorarius longicaudus</i>
23 Nov 1994	25°13'S, 44°52'W	-	3	-
25 Nov 1994	25°15'S, 44°55'W	2	-	-
26 Nov 1994	25°10'S, 45°03'W	1	-	-
24 Mar 1995	25°58'S, 45°34'W	1	-	-
25 Mar 1995	25°54'S, 45°34'W	5	2	-
25 Mar 1995	27°05'S, 46°47'W	5	5	1
26 Mar 1995	27°06'S, 46°50'W	4	1	-
26 Mar 1995	27°03'S, 46°46'W	2	-	-
27 Mar 1995	27°03'S, 46°46'W	8	2	-
27 Mar 1995	27°49'S, 46°17'W	-	1	-
28 Mar 1995	27°49'S, 46°17'W	4	1	-
28 Mar 1995	27°47'S, 47°12'W	5	3	-
29 Mar 1995	27°58'S, 47°09'W	6	-	-
29 Mar 1995	27°04'S, 46°49'W	5	2	-
30 Mar 1995	27°07'S, 46°52'W	14	2	-
30 Mar 1995	25°54'S, 45°35'W	4	-	-
30 Mar 1995	25°12'S, 45°07'W	2	3	-
30 Mar 1995	25°06'S, 45°15'W	6	-	-
3 Oct 1996	26°49'S, 46°46'W	1	-	-
8 Oct 1996	25°39'S, 45°08'W	1	-	-
27 May 1997	24°41'S, 44°37'W	1	-	-
28 May 1997	24°07'S, 43°43'W	7	-	-
28 May 1997	24°14'S, 43°44'W	2	-	-

Most recorded skuas were immatures (first-third summer plumage) and very few probably adult birds with all dark underwings were seen, suggesting that Brazilian waters are mainly visited by young birds. The records suggest that Pomarine Skuas are more common off Brazil than expected from previous accounts. The rich waters of the Falklands/Malvinas Current and the coasts of Uruguay and Argentina are some of the main areas used by Long-tailed *Stercorarius longicaudus* and Arctic *S. parasiticus* skuas during the austral summer (Veit 1995, Malling Olsen & Larsson 1997), both being regularly recorded in southern Brazil (Vooren & Chiaradia 1989). Olog (1967) and Escalante (1970, 1972, 1985) suggested the regular presence of Pomarine Skuas in Uruguay and Argentina, and my data agree with their view that Pomarine Skuas are regular migrants to the southern West Atlantic.

In Brazil, several seabirds have been documented only from a few beached corpses, suggesting they are quite rare. However, very few ornithologists have attempted to study seabirds in their open-sea habitat at and beyond the Brazilian shelf. Recent offshore studies showed that several species,

such as the Pomarine Skua, were in fact quite common, for example around fishing vessels (Olmos 1997, Olmos *et al.* 2001).

Observations were made aboard the *R/V Orion* and the *F/V Mar Paraíso* and *Margus II*. My thanks to their crews and skippers. The *F/V Margus II* were part of Project REVIZEE. My thanks to Gastão C. C. Bastos (Instituto de Pesca, SP) for including me in the cruises and for his help during them. Kees Camphuysen, Richard Veit and an anonymous referee made substantial improvements in the manuscript.

MIDDELSTE JAGERS *STERCORARIUS POMARINUS* OVERWINTEREND VOOR BRAZILIË

Tot dusverre werden Middelste Jagers Stercorarius pomarinus vrijwel niet in zuidelijk Zuid-Amerika gemeld. Waarnemingen vanaf vissersschepen op zee toonden aan dat Middelste Jagers op het Continentale Plat van Brazilië (23°30'ZB en 29°ZB) voorkomen in maart, mei, oktober en november. In juli werden tot dusverre geen Middelste Jagers gezien, maar in de andere maanden was het zelfs de talrijkste soort. De hoogste aantallen werden in maart gezien, met maximaal 14 exemplaren in een groep. Vrijwel alle vogels waren onvolwassen. Het voorkomen van Middelste Jager is veel regelmatig dan de literatuur suggereert.

REFERENCES

- Belton W. 1994. Aves do Rio Grande do Sul: distribuição e biologia. Editora UNISINOS, São Leopoldo.
- Escalante R. 1970. Aves marinas del Rio de la Plata y aguas vecinas del Oceano Atlántico. Barreira y Ramos, Montevideo.
- Escalante R. 1972. First Pomarine Skua specimen from Brazil. *Auk* 89: 663-665.
- Escalante R. 1985. Los salteadores menores (*Stercorarius parasiticus* y *S. longicaudus*) en el Uruguay. *Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo* 154(11): 1-8.
- Furness R.W. 1987. The skuas. T & AD Poyser, Calton.
- Malling Olsen K. & Larsson H. 1997. Skuas and jaegers: a Guide to the Skuas and Jaegers of the world. Yale University Press, New Haven and London.
- Olmos F. 1997. Seabird flocks attending bottom long-line fishing off southeast Brazil. *Ibis* 139: 685-691.
- Olmos F. 2000. Revisão dos registros de *Stercorarius pomarinus* no Brasil, com notas sobre registros de *S. longicaudus* e *S. parasiticus* (Charadriiformes: Stercorariidae). *Nattereria* 1: 29-33.
- Olmos F., Neves T.S. & Bastos G.C.C. 2001. A pesca com espinhéis e a mortalidade de aves marinhas no Brasil. Pp. 327-337 *In* Albuquerque J., Cândido J. F., Straube F. C. & Roos A. (orgs.) *Omitologia e Conservação: da Ciência às Estratégias*. SBO, UNISUL/CNPq.
- Olrog C.C. 1967. Observaciones sobre aves migratorias del Hemisferio Norte. *Hornero* 10: 292-298.
- Silva A.O.A. 2000. A pesca com espinhel de fundo no Estado de São Paulo. <http://www.setorpesqueiro.com.br/pesquisas/espinhel.htm>
- Tutui S.L.S., Bastos G.C.C., Tomás A.R.G., Tiago G.G. & Zavala-Camin L. A. 2000. Species composition of the exploratory fisheries with bottom longline off southeast Brazil. *Ciência e Cultura* 52: 55-58.
- Veit R.R. 1995. Long-tailed Skuas wintering along the Falkland Current. *American Birds* 39: 873-878.
- Vooren C.M. & Chiaradia A. 1989. *Stercorarius longicaudus* and *S. parasiticus* in southern Brazil. *Ardea* 77: 233-235.

AT-SEA RECORDS OF CAPE VERDE
SHEARWATERS *Calonectris edwardsii* IN
BRAZIL

FÁBIO OLMOS

Olmos F. 2002. At-sea records of Cape Verde Shearwaters Calonectris edwardsii in Brazil. Atlantic Seabirds 4(2): 77-80. This note reports several sightings of Cape Verde Shearwaters Calonectris edwardsii off Brazil in an area where they have not been previously reported. Cape Verde Shearwaters were assumed to disperse in the South Atlantic Ocean outside the breeding season, while only several strandings indicated that this species occurred off South America.

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The Cape Verde Shearwater *Calonectris edwardsii* is endemic to the Cape Verde Islands. During the 1990s, its total population was estimated at c. 10,000 pairs (Hazevoet 1994, 1995). Although described as a distinct taxon by Oustalet (1883), it was virtually ignored during much of the 20th century, presumably at least partly due to its alleged lowly status of being 'merely a subspecies' of *C. diomedea*. Recently, renewed attention has been given to its distinctive characters (Hazevoet 1995), which make it relatively easy to identify even at sea (Porter *et al.* 1997). Other *Calonectris* shearwaters breed in the northern Macaronesian islands (*borealis*) and the Mediterranean (*diomedea*) and these are believed to be transequatorial migrants to the western South Atlantic off southern Brazil, Uruguay, and Argentina, and to South Africa and the Indian Ocean (e.g. Mougin *et al.* 1988, Ristow *et al.* 2000). Migration routes and wintering areas of *edwardsii* are poorly known and it has been suggested that it disperses into the western South Atlantic (Bourne & Curtis 1985). The southernmost observation to date is of three at 38°36'S, 53°30'W, off Argentina (Curtis 1994). Several recoveries of beached birds in Brazil (Lima *et al.* 1997, Petry *et al.* 2000) have supported the view that the taxon's main wintering grounds are to be found in the western South Atlantic off South America. In this note I report on recent at sea observations of *C. edwardsii* off Brazil and also comment on identification of the taxon.

I recorded the first Cape Verde Shearwaters while aboard the RV *Orion*, which was setting bottom long-lines between the coasts of São Paulo and Santa Catarina. Two *Calonectris* shearwaters persistently followed the vessel on 25 March 1995 during the early morning setting, and one was photographed

later the same day at 27°05'S, 46°47'W. Additional records were made aboard the FV *Margus II*, another long-liner then fishing on the Brazilian shelf off Paraná and São Paulo states. In the morning of 27 May 1997, at 25°52'S, 44°36'W, two *Calonectris* shearwaters followed the boat during line setting. They were about the same size or smaller than the four Great Shearwaters *Puffinus gravis* seen with them, had slim bodies and proportionally long tails, and had noticeably dark bills. During line hauling, about four hours later, another small *Calonectris* (or one of the birds seen before) joined the seabird flock feeding on the discards at 24°47'S, 44°32'W. Depth at this point was 386 m. The following day I again observed a small *Calonectris* attending the boat during line setting. This time one Atlantic Cory's Shearwater *Calonectris* [*diomedea*] *borealis* and 32 Great Shearwaters were also following the boat, allowing direct comparisons in size. Likewise Great Shearwaters, the small *Calonectris* sat on the water waiting for bait scraps (the Cory's Shearwater rarely did that), and was seen to lose its food to Pomarine Skuas *Stercorarius pomarinus* twice. The small *Calonectris*, the Cory's and the Great Shearwaters kept with the boat during the entire line hauling. The long-line stretched from 24°07'S, 43°48'W to 24°06'S, 43°44'W, in waters 150 m deep.

Cape Verde Shearwater 28 May 1997 at 24°06'S, 43°44'W Kaapverdische
Pijlstormvogel 28 mei 1997 24°06'ZB, 43°44'WL. (F.Olmos)

Pictures taken of birds seen in 1995 and 1997 show small, slim-bodied *Calonectris* with longish tail, thin bill with a dark point, and uppertail-coverts with white, all consistent with Cape Verde Shearwaters (Porter *et al.* 1997). Similar birds were later seen during a cruise aboard the pelagic long-liner FV *Taihei Maru* operating off the shelf (waters deeper than 2 500 m) of Santa Catarina state. One probable Cape Verde Shearwater passed by the boat on 3 July 2001 at 27°50'S, 45°49'W (water temperature 21.5°C) and later what may have been the same bird was seen at 27°32'S, 46°15'W (water temperature 22.4°C). In both sightings my attention was drawn to the dark dorsal aspect of the bird(s), its slim body and the long tail, both recalling Wedge Tailed-Shearwaters *Puffinus pacificus* I had seen previously in the northern Pacific. Although no size comparison to other seabirds could be made, I believe both sightings refer to Cape Verde Shearwater. Porter *et al.* (1997) also mention the resemblance of Cape Verde Shearwater body shape to Wedge-tailed Shearwaters.

The Brazilian records of Cape Verde Shearwaters suggest that at least some individuals migrate to the same wintering areas as Cory's Shearwaters and Manx Shearwaters *Puffinus puffinus*. Further observations made both at-sea and on beach derelicts may well prove Cape Verde Shearwaters to be regular migrants to the South American coast.

C.J. Hazevoet kindly checked the identity of the 1995 bird. Bernard Zonfrillo and Kees Camphuysen made useful suggestions on an earlier draft of this note.

WAARNEMINGEN VAN KAAPVERDISCHE PIJLSTORMVOGELS
CALONECTRIS EDWARDSII VOOR DE KUST VAN BRAZILIË

Het is niet bekend waar Kaapverdische Pijlstormvogels *Calonectris edwardsii* na de broedtijd heen trekken, maar aangenomen wordt dat zij zich over de Zuid-Atlantische Oceaan verspreiden. Er waren verschillende strandingen op de Braziliaanse kust, bekend maar verder waren er geen aanwijzingen waaruit bleek dat deze soort in de kustwateren van Brazilië voorkwam. In deze notitie worden enkele waarnemingen gedocumenteerd van Kaapverdische Pijlstormvogels die zich gedurende enige tijd rond lijnenvissers voor de kust van Brazilië ophielden. Vrijwel alle vogels konden worden gefotografeerd en de determinaties zijn door experts (CJH, BZ) bevestigd. De auteur noemt de kenmerken die de aandacht trokken en welke gebruikt werden bij de identificatie. De gegevens suggereren dat deze soort regelmatig in Brazilië voorkomt.

Bourne W.R.P. & Curtis W.F. 1985. South Atlantic seabirds. *Sea Swallow* 34: 18-28.

Curtis W.F. 1994. Further South Atlantic records. *Sea Swallow* 43: 19-28.

Hazevoet, C.J. 1994. Status and conservation of seabirds in the Cape Verde Islands. In: D.N. Nettleship, J. Burger & M. Gochfeld (eds.), *Seabirds on Islands – Threats, Case studies and Action Plans*. Pp. 279-293. BirdLife Conservation Series No. 1. BirdLife International, Cambridge, U.K.

Hazevoet C.J. 1995. The birds of the Cape Verde Islands. BOU Check-list 13, Tring.

Lima P.C., Lima R.C.F.R., Fonseca-Neto F.P. & Santos S.S. 1997. Ocorrência e mortalidade de aves oceânicas no litoral baiano em 1996, e segundo encontro de *Phoebetria fusca* (Hilsenberg,

- 1822) para o Brasil. Resumos do VI Congresso Brasileiro de Ornitologia, Belo Horizonte, p. 77.
- Mougin J.-L., Jouanin C. & Roux F. 1988. Les migrations du Puffin cendré *Calonectris diomedea*. L'Oiseau R.F.O. 58: 303-319.
- Olmos F. & Martuscelli P. in press. Répteis, aves e mamíferos marinhos do litoral sul de São Paulo. In O.A.V. Marques, W. Duleba & F.D. Por (org.). Ambiente, flora e fauna da Estação Ecológica Juréia-Itatins.
- Oustalet E. 1883. Description d'espèces nouvelles d'oiseaux provenant des îles du Cap-Vert. Ann. Sci. Nat. (Zool.) 16 (5): 1-2.
- Petry M.V., Bugoni L. & Fonseca V.S.S. 2000. Occurrence of the Cape Verde Shearwater *Calonectris edwardsii* on the Brazilian coast. Bull. Brit. Orn. Club 120(3): 198-200.
- Porter R., Newell D., Marr T. & Jolliffe R. 1997. Identification of Cape Verde Shearwater. Birding World 10: 222-228.
- Ristow D., Berthold P., Hashmi D. & Querner U. 2000. Satellite tracking of Cory's Shearwater migration. Condor 102: 696-699.
- Warham J. 1996. The behaviour, population biology and physiology of the petrels. Academic Press, London.