

## 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 (Arnason 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. Arnason (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 km<sup>2</sup> 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

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		$\chi^2$	P
	n	% success	n	% success		
Common Guillemot	920	10.4	501	10.58	0	n.s.
All other species <sup>1</sup>	59	5.08	33	3.03	0.2	n.s.

<sup>1</sup>Comprising Razorbill, Atlantic Puffin, Black-legged Kittiwake and Northern Fulmar.

birds: 'pale-phase' or 'light-phase' birds (these two terms are interchangeable) 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

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	$\chi^2$	<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	<i>n.s.</i>

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.

**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

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	$\chi^2$	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.

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 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

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		$\chi^2$	$P$
	n	% success	n	% success		
All conditions	381	10.5	203	11.82	0.19	n.s.
Grey <sup>1</sup> sky	170	7.65	71	7.04	0.02	n.s.
White <sup>1</sup> 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	$\chi^2$	$P$
< 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.

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 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

*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)

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%.

**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.

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#### KLEURFASSEN 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.

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