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EVOLUTION OF REVERSED SEXUAL SIZE DIMORPHISM IN SKUAS AND JAEGERS

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ABSTRACT.—Skuas and jaegers (Stercorariinae), like other birds with a raptorial lifestyle, display reversed sexual dimorphism in size (RSD) in which females are larger than males. This condition is commonly believed to be associated with the morphology or behavioral ecology of avian predators, and numerous theoretical explanations have been presented to account for its evolution. Most tests of these ideas have been theoretical or based on comparative analyses. We present tests of specific hypotheses of RSD based on field studies of Great Skuas (*Catharacta skua*) and Parasitic Jaegers (*Stercorarius parasiticus*) breeding in Shetland. We also present a comparative analysis of foraging behavior and degree of RSD within the Stercorariinae. We found no support for the popular theories that claim that RSD evolved as a result of specialized roles during breeding. Large females were not more fecund, nor were they the main defenders of the nest. Male body size was not correlated with any breeding parameter. In addition, interspecific comparisons did not support the idea that the degree of RSD is related to foraging behavior during the breeding season (as opposed to morphology). Female dominance within pairs did not affect any breeding parameters. Support was found for theories that RSD is linked to sexual selection. Large females had an advantage when pairing with older males, which could be a result of intrasexual competition for mates. There was assortative mating for size, indicating that small males could also have an advantage in pairing, because large males seem to be rejected by small females. Given the disparate results of several previous studies, we conclude that a large body of empirical evidence will be needed before we can draw firm conclusions about the main selective factors that act to maintain current levels of RSD in natural populations of raptorial birds. *Received 24 July 1997, accepted 18 June 1998.*

THE MECHANISMS behind the origin and maintenance of sexual size dimorphism in animals are poorly known (Hedrick and Temeles 1989). Several unrelated groups of birds display reversed sexual dimorphism in size (RSD; females larger than males), suggesting that this condition evolved independently on a number of occasions (Jehl and Murray 1986, Paton et al. 1994). Reversed size dimorphism is a common feature of some avian groups with a raptorial lifestyle, principally the diurnal and nocturnal birds of prey, skuas and jaegers, and frigatebirds. This has led to the belief that the evolution of reversed size dimorphism is linked to the morphology or behavioral ecology of avian predators, regardless of its evolutionary origin in other taxa.

Many hypotheses attempt to explain RSD in birds of prey (see Mueller 1990). Proposed advantages of large female size include greater ability to produce and incubate eggs, protect the nest, and care for offspring (Andersson and Norberg 1981, Wheeler 1983, Lundberg 1986, Jönsson and Alerstam 1990), and superiority in intrasexual competition for mates (Olsen and Olsen 1987, Newton 1988). It has also been suggested that small males have greater foraging efficiency (Andersson and Norberg 1981, Lundberg 1986, Jönsson and Alerstam 1990, Hakkarainen and Korpimäki 1991) and superiority in territorial contests or nuptial displays (Widén 1984, Safina 1984). Another group of hypotheses states that it is the relative asymmetry within pairs that is advantageous, not male or female size per se. Female dominance resulting from RSD should facilitate rapid pairing and could help females to relegate their partner to the role of food provider (Smith 1982).

The above theories predict a correlation between body size and mating or breeding success in at least one sex. This would be counter-

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balanced by differential mortality of phenotypes, because it is unlikely that the optimal size from the perspective of breeding-role specialization would be the same as that which maximizes postfledging and overwinter survival (Owens and Bennett 1994). Nonetheless, it should be possible to detect directional selective pressures on body size operating during the breeding season (Hedrick and Temeles 1989, Ydenberg and Forbes 1991).

Compared with the vast number of theoretical and comparative analyses published on RSD, few studies of raptorial species have attempted to relate body size to the performance of individuals during reproduction. Several authors have examined mating in relation to size (Newton 1983, Bowman 1987, Marti 1990, Bortolotti and Iko 1992, Plumton and Lutz 1994, Hakkarainen et al. 1996), but attempts to relate breeding success and foraging efficiency to body size are scarce and have produced mixed results (Newton 1988; Hakkarainen and Korpimäki 1991, 1995; Hakkarainen et al. 1996). Given that the adaptive values of phenotypes are likely to change in variable environments (Hakkarainen and Korpimäki 1995), and that contemporary selective pressures might be weak, a large amount of empirical evidence will be needed before any firm conclusions can be extracted from this type of study.

All seven species of skuas and jaegers (subfamily Stercorariinae) display RSD (Furness 1996), unlike their close relatives, the gulls (subfamily Larinae). Similar to the birds of prey, skuas and jaegers also have a pronounced division of roles between the sexes during most of the breeding season (Pietz 1987; Furness 1987, 1996; Caldow 1988; Catry and Furness 1997a; Phillips and Furness 1997a; but see Pietz 1986). Males feed their partners during egg formation (i.e. courtship feeding) and do most of the foraging during incubation and, in several species, during chick rearing. Unlike some raptors, they also carry out a substantial part of the incubation. As the season advances, females progressively increase their contribution in terms of foraging effort, and after the first days or weeks of chick rearing, they spend almost as much time gathering food as do their mates. Skuas and jaegers feed mostly on fish, birds, and small mammals but are versatile in their foraging techniques, acting as predators, scavengers, and kleptoparasites (Furness 1987; Phillips et al. 1996b, 1997). Some species, such as the Great Skua (*Catharacta skua*), have an ecological niche very similar to that of the large gulls (*Larus* spp.). One important difference between skuas and gulls is morphological. Skuas and jaegers have hooked claws that allow them to grab birds in flight or hold them on the ground, although not to carry them (Furness 1987, 1996).

Often breeding colonially (although defending small territories), skuas and jaegers are particularly suited for tests of hypotheses of RSD. A large number of pairs can be studied simultaneously, and because in many populations (including those in the United Kingdom) no feeding territories are defended, territory quality is not usually a confounding factor when analyzing mate preferences or breeding performance. The large number of conspecifics in a small area also could allow birds to be more selective in their choice of partner. Here, we incorporate field observations of skuas of known size to test hypotheses related to RSD. We studied two species, one in each genus (*Catharacta* and *Stercorarius*) in the subfamily. We also present a comparative analysis of foraging behavior and degree of RSD within the Stercorariinae using published information. Our taxonomic classification within the Stercorariinae follows Furness (1996). It is not our aim to present an extensive review and discussion of all current hypotheses for the evolution of RSD in raptorial birds, nor to draw any general conclusions. Instead, we concentrate our efforts toward evaluating hypotheses for which our data allow robust tests of specific predictions.

STUDY AREA AND METHODS

Breeding data were collected in Foula, Shetland (60°08′N, 2°05′W) for Parasitic Jaegers (*Stercorarius parasiticus*) between 1993 and 1994 and for Great Skuas between 1994 and 1996. Breeding territories of individually color-banded birds were visited daily or on alternate days early in the season, and the presence of newly laid eggs was determined by watching for the initiation of mobbing by the adults (or distraction behavior in the case of Parasitic Jaegers) and then locating and checking the nest. Most females lay two eggs at an interval of two to three days between eggs. Laying dates for nests that were not located until after clutch completion were back-dated from hatching dates of the first or only chick, assuming an incubation period of 26 days for Parasitic Jaegers and 29 days for Great Skuas.

TABLE 1. Correlations between PC1 scores and morphometric variables in Great Skuas and Parasitic Jaegers.

Variable	Great Skuas		Parasitic Jaegers	
	Males	Females	Males	Females
Tarsus length	0.61	0.58	0.80	0.85
Wing length	0.54	0.59	0.76	0.36
Head length	0.58	0.57	0.62	0.81
Sample size	112	127	77	107
% Variance explained	60.0	51.0	53.6	50.2

Nests and eggs were marked, eggs measured using vernier calipers (±0.1 mm), and the volume (mL) of each egg calculated as $0.00048 \times \text{length} \times \text{breadth}^2$ (Coulson 1963). Hatching success and chick survival were recorded by visiting marked nests at regular intervals throughout incubation, every one to two days around hatching, and approximately every 6 to 10 days during chick rearing. Great Skua chicks older than 30 days were considered to have fledged because only 3.8% of chicks disappear or are found dead between then and the normal fledging age of approximately 45 days (Phillips et al. 1997). Because adult skuas and jaegers have high survival and low divorce rates, breeding data collected in consecutive years from the same pair cannot be considered statistically independent. Therefore, most of the following analyses were carried out separately for each year.

Adult Parasitic Jaegers and Great Skuas were trapped, weighed, and measured during the breeding season. All Great Skuas were measured by PC and Parasitic Jaegers by RAP. The sex of Great Skuas was determined by observation of courtship feeding and copulations. The sex of Parasitic Jaegers was determined by behavioral observations, by a hierarchical combination of two discriminant functions based on the prior probabilities of group membership (with an accuracy of >91% for birds classified), by dissection of birds found dead at the colony, or by association with a partner sexed by one of these methods (Phillips and Furness 1997b). For each sex and species, a separate principal components analysis (Rising and Somers 1989) incorporating the morphometric variables wing length, tarsus length, and head length (including the bill) was used to produce single-factor scores (PC1 scores) representing body size (Table 1). Body mass was not used as a measure of size because it also reflects body condition. The age of some Great Skuas could be determined because they had been marked as chicks.

Male and female morphometric and composite body-size indices (PC1) were compared within pairs to test for evidence of assortative mating with respect to size. Differences in structural size among males or females, or in the degree of dimorphism within the pair, may be important determinants of breeding phenology and success. Tests were performed to see if either laying date or clutch volume (two-egg clutches only) was correlated with adult size or dimorphism indices. We used the dimorphism index (DI; Marti 1990):

$$\text{DI} = (\text{female size} \pm \text{male size})/(\text{female size} + \text{male size}), \quad (1)$$

except for PC1 scores, because independent PCAs were derived for each sex, making it impossible to scale the index to the size of the pair. For PC1 scores, the dimorphism index was simply given by female size minus male size. These two indices are effectively almost the same, and, for simple measurements (e.g. wing length) they are very strongly correlated in our samples (Pearson's $r > 0.999$ for all variables measured; $n = 61$ Great Skua pairs and 65 Parasitic Jaeger pairs). We used ordinal logistic regression to compare the number of chicks fledged with adult size and pair dimorphism. This allows the dependent variable to take more (ordinal) values than two, as in simple logistic regressions. Significance levels of these regressions were assessed using log-likelihood ratio tests (G^2 statistic).

Nest defense behavior in birds varies a great deal even within species, depending on parental quality, offspring number, nest-site characteristics, and type of predator (see Montgomerie and Weatherhead 1988, Redondo 1989). In both Great Skuas and Parasitic Jaegers, the intensity of the response to humans should be broadly representative of that toward other mammalian nest predators, given the history of both egg harvesting and persecution in Shetland (Furness 1987).

For each species, nest defense behavior of marked pairs was scored when both partners were present, because single birds are noticeably less aggressive (Furness 1987). Jaeger nest defense was scored at two stages of the season and skua nest defense at four stages. The observer (PC for Great Skuas and RAP for Parasitic Jaegers) walked directly toward the nest with head bowed, stood at the nest for 60 s, and then left the breeding territory. For each pair of Great Skuas we recorded: (1) which of the birds was the more aggressive (i.e. came closer to the observer while swooping), and (2) whether or not each of the birds hit the observer on the head. Compared with Great Skuas, which show a more variable response, the ma-

TABLE 2. Measurements of Great Skuas and Parasitic Jaegers ($\bar{x}$ ± SD, with n in parentheses) captured at Foula. Samples do not include birds sexed by discriminant analysis.

Variable	Males	Females	t	P
		Great Skua		
Wing chord (mm)	416.8 ± 7.1 (112)	427.4 ± 7.1 (127)	11.5	<0.001
Tarsus (mm)	68.9 ± 1.55 (112)	70.3 ± 1.72 (127)	6.7	<0.001
Head (mm)	109.9 ± 1.68 (112)	111.5 ± 1.82 (127)	7.0	<0.001
Body mass (g)	1,271 ± 69.4 (112)	1,409 ± 75.0 (125)	14.6	<0.001
		Parasitic Jaeger		
Wing chord (mm)	320.3 ± 5.0 (44)	327.2 ± 5.9 (53)	6.1	<0.001
Tarsus (mm)	44.5 ± 1.13 (44)	45.2 ± 1.81 (53)	2.2	<0.05
Head (mm)	76.1 ± 1.55 (43)	77.4 ± 1.53 953)	4.0	<0.001
Body mass (g)	405.0 ± 26.8 (32)	466.8 ± 30.2 (42)	9.1	<0.001

jority of Parasitic Jaegers hit the observer. Consequently, the total number of swoops by marked Parasitic Jaegers was recorded. In addition, we noted the intensity of distraction behavior of Parasitic Jaegers, again only when both birds in a pair were present. Distraction intensity was scored on a scale of 0 to 5: 0 = no distraction; 1 = walking away, possibly bowing, wings not extended; 2 = standing with outstretched wings or occasional flapping; 3 = walking with outstretched wings or occasional flapping; 4 = walking or standing with vigorous flapping; and 5 = running with vigorous flapping. These are essentially points on a continuos scale, but in practice it was fairly straightforward to assign a bird to one of these categories.

RESULTS

Female and male size.—Measurements of live skuas and jaegers are presented in Table 2. Incubation masses were compared for Parasitic Jaegers because females, but not males, show a stepwise reduction in mass shortly after the chicks hatch (Phillips and Furness 1997a). Females were significantly larger than males in all traits studied.

Assortative mating in relation to size and age.—For the analyses below, we combined data from several years, but each pair contributed a single data point. Female and male body sizes (PC1 scores) were positively correlated within pairs of Parasitic Jaegers ($r = 0.28, n = 67, P = 0.027$). A similar positive correlation occurred in Great Skua pairs ($r = 0.22, n = 61, P = 0.085$), but it was not statistically significant.

In Great Skuas, adult body size was not correlated with age in males ($r = 0.16, n = 41, P = 0.31$) or females ($r = 0.18, n = 48, P = 0.22$). The same was true for Parasitic Jaegers (Phillips and Furness 1997b). In Great Skuas, female size and male age were positively correlated (Spearman $r = 0.38, n = 50, P < 0.01$), as were male size and female age (Spearman $r = 0.32, n = 44, P < 0.05$). Skuas that provided data for the tests were between 5 and 29 years old. Not enough known-age birds were available to test these relationships in Parasitic Jaegers.

Body size, dimorphism, and breeding performance.—Breeding performance during our study was neither very high nor very low. Parasitic Jaegers successfully raised 0.97 and 0.90 chicks per pair in 1993 and 1994, respectively (Phillips et al. 1996a). Great Skuas raised 0.86 chicks per pair in 1994 and 1.13 in 1995 (Phillips et al. 1997). In both species, neither female nor male size affected laying date (Table 3). Only female body size had an effect on clutch volume: large females laid larger eggs, although the trend in Great Skuas was not significant in every year (Table 3). In general, body size had no effect on hatching or breeding success (Table 4). In 1995 only, body size of male Great Skuas was negatively correlated with the number of chicks hatched. However, this did not result in higher overall productivity by small males in that year (Table 4). The results were unchanged when we repeated the above analyses using univariate measurements (wing, tarsus, and head plus bill length) instead of PC1 scores.

Pairs of Parasitic Jaegers with a large dimorphism index tended to lay early in the season in 1993 (Table 3). Apart from this effect, the degree of size dimorphism within pairs was not correlated with laying date, clutch volume, hatching success, or fledging production in either of the two species (Tables 3 and 4). Again, the same results were obtained when we re-

TABLE 3. Correlations between body size and pair dimorphism with laying date and clutch volume in Great Skuas and Parasitic Jaegers.

	Laying date				Clutch volume			
	1993	1994	1995	1996	1993	1994	1995	1996
				Great Skua				
Male size								
PC1	—	−0.16	−0.10	−0.18	—	−0.23	−0.06	0.00
n	—	42	91	99	—	39	91	89
Female size								
PC1	—	0.08	−0.10	−0.10	—	0.18	0.31**	0.16
n	—	61	100	100	—	50	89	90
Pair dimorphism								
PC1	—	−0.20	0.07	0.02	—	−0.27	−0.27	−0.17
n	—	30	47	49	—	24	39	40
				Parasitic Jaeger				
Male size								
PC1	−0.18	−0.05	—	—	−0.07	−0.02	—	—
n	56	68	—	—	54	62	—	—
Female size								
PC1	0.16	0.02	—	—	0.30*	0.23*	—	—
n	70	87	—	—	64	77	—	—
Pair dimorphism								
PC1	−0.44*	−0.12	—	—	−0.08	−0.08	—	—
n	33	56	—	—	32	51	—	—

*, $P < 0.05$; **, $P < 0.01$.

TABLE 4. Effects of male and female size and pair dimorphism on hatching success (number of eggs hatched) and breeding success (number of chicks fledged) in Great Skuas and Parasitic Jaegers. Data assessed by ordinal logistic regression; test statistic is G^2 with one degree of freedom.

	No. of chicks hatched		No. of chicks fledged	
	1994	1995	1994	1995
	Great Skuas			
PC1 males	0.30	6.73*	0.07	1.23
n	41	93	37	90
PC1 females	0.16	1.01	0.12	1.29
n	56	98	47	91
Dimorphism	1.23	1.11	0.00	0.70
n	28	46	25	44
	Parasitic Jaegers			
PC1 males	0.00	0.34	0.04	0.33
n	56	68	53	62
PC1 females	0.32	1.06	0.14	0.80
n	71	87	68	77
Dimorphism	1.74	0.00	0.00	0.70
n	33	56	31	52

*, $P < 0.01$ (small males hatched more chicks).

peated the analyses using univariate morphometric measurements instead of composite body-size indices.

Male and female roles in nest defense.—We compared aggression levels of male and female Great Skuas at four different stages of the nesting cycle (Table 5). Males were the more aggressive nest defenders in periods 1 ($\chi^2 = 59.1$, df = 1, $P < 0.0001$), 2 ($\chi^2 = 12.2$, df = 1, $P < 0.001$), and 3 ($\chi^2 = 6.2$, df = 1, $P < 0.05$) but not in period 4 ($\chi^2 = 2.7$, df = 1, $P > 0.10$). Aggression levels of female Great Skuas increased progressively from egg laying to hatching ($\chi^2 = 40.7$, df = 6, $P < 0.001$; Table 5). In a sample of 14 individual pairs for which we measured aggression in periods 1 and 2, females increased absolute aggression levels (from not swooping to swooping) from period 1 to 2 in seven cases, whereas males did so only once (Fisher exact test, $P = 0.02$). Male and female Parasitic Jaegers did not differ significantly in the intensity of distraction behavior or in the number of swoops at the observer at either stage of the season (Table 6).

RSD and foraging behavior in different species of Stercorariinae.—It is well known that in diurnal

TABLE 5. Relative levels of aggression of male and female pairs of Great Skuas.

Period	Most aggressive bird in pair (%)			
	Male	Female	Neither	*n*
(1) After laying one egg	91.4	1.5	7.1	70
(2) After laying two eggs	59.4	6.2	34.4	32
(3) Half-way into incubation	49.1	18.8	32.1	53
(4) At hatching	51.1	27.8	21.1	47

raptors, species that usually catch relatively agile prey (e.g. birds vs. mammals or mammals vs. insects) show greater size dimorphism (Newton 1979). It has been suggested that RSD evolved because small size confers the advantage of greater aerial agility to the sex (male) undertaking the bulk of food provisioning for the mate and brood. Small size would also lower seasonal energy consumption for birds spending long periods in flight. In Table 7, we present a brief summary of the foraging techniques and degree of RSD in different skua and jaeger species. We could not find enough suitable data for the Chilean Skua (*Catharacta chilensis*) or the Falkland Skua (*C. antarctica antarctica*). It appears that skuas and jaegers exhibit a similar level of wing and body mass dimorphism in spite of marked differences in foraging style (Table 7).

DISCUSSION

Are large females better parents?—It has been suggested that in species with RSD, larger females should be more fecund or provide better care to offspring (Andersson and Norberg 1981, Wheeler 1983, Lundberg 1986). Skuas and jaegers have a relatively fixed clutch size, with most clutches being composed of two eggs (Furness 1987, 1996). We report that large females lay slightly larger eggs. However, this effect is also found in species with "normal" size dimorphism (i.e. males larger than females; Loman 1984) and cannot, by itself, explain RSD in skuas and jaegers. In addition, egg size had only a weak effect on Great Skua chick survival in the first four days after hatching (Furness 1983), and clutch volume of two-egg clutches was not correlated with breeding success in the years studied (Catry and Furness 1997b). Other possible advantages of large female size include a greater ability to store energy reserves and protect developing ovarian follicles. Larger females could also be better at incubation, either because of an improved ability to physically cover the eggs or a higher resistance to fasting while their partners forage. If these hypotheses were correct, large females would lay early in the season, produce eggs of high quality, and / or incubate more efficiently, with a resultant increase in hatching success. However, we found no significant relationships between female size and laying date or hatching success in either Great Skuas or Parasitic Jaegers, despite large sample sizes. Still, it must be kept in mind that such relationships might only be strong enough to be detected in some years, depending on environmental conditions.

In most species of raptors, skuas, and jaegers, females spend more time on the territory during incubation and chick rearing than do males, and it could be that large female size has

TABLE 6. Relative levels of aggression of male and female Parasitic Jaegers. Sample sizes in parentheses.

Period	Male	Female	Z^a	*P*
	Median intensity of distraction display			
(1) Half-way into incubation	2 (64)	2 (82)	0.00	>0.05
(2) At hatching	2 (46)	2 (55)	1.15	>0.05
	Mean (± SD) number of swoops at observer			
(1) Half-way into incubation	3.4 ± 5.6 (63)	3.8 ± 5.8 (81)	0.13	>0.05
(2) At hatching	5.9 ± 6.0 (46)	5.4 ± 6.3 (55)	0.79	>0.05

[a] Mann-Whitney *U*-test comparing differences between sexes.

TABLE 7. Main foraging modes during the breeding season and degree of size dimorphism of different skua and jaeger species. All morphological data from Furness (1987), except where indicated. Behavioral data from Cramp and Simmons (1983), Furness (1987, 1996), Pietz (1987), Young et al. (1988), and Phillips et al. (1996a, 1997).

	Foraging mode			Dimorphism index	
Species	Walking	Flying	Aerial chasing	Body mass	Wing length
Catharacta skua		+	+	5.3	1.3
Catharacta skua[a]		+	+	5.3	1.2
Catharacta maccormicki	+	+		5.2	0.7
Catharacta antartica hamiltoni	+			5.1	1.3
Catharacta antartica lonnbergi	+			6.1	0.8
Stercorarius pomarinus	+	+		6.4	1.5
Stercorarius parasiticus		+	+	7.6	0.9
Stercorarius parasiticus[a]		+	+	7.1	1.1
Stercorarius longicaudus		+		5.7	0.6

[a] This study.

evolved because of the female's crucial role in the defense of eggs and young. This hypothesis assumes that large birds are more efficient in deterring predators. Within pairs of Great Skuas, however, males generally display the more aggressive behavior toward humans than do females. Indeed, female Great Skuas were particularly unaggressive toward humans during and immediately after egg laying, which is a time when they undertake the greater share of incubation duties. The level of nest defense (either mobbing or distraction behavior) did not differ between male and female Parasitic Jaegers. The lack of a strong aggressive behavior during egg laying could have evolved to prevent a developing egg from breaking inside the female's body. Studies of diurnal and nocturnal raptors also showed the male to be the primary defender of the nest (Wiklund and Stigh 1983, Andersson and Wiklund 1987). It is quite possible that small size and increased maneuverability of males allow them to come closer and strike potential predators with a reduced risk of a retaliatory attack (Andersson and Wiklund 1987). Although large female size could be favorable in confrontations with some kinds of predators, it seems unlikely that this advantage would be large enough to compensate for the generally low level of aggressiveness in female skuas and jaegers.

Are small males better parents?—In skuas, jaegers, and raptors, males undertake the bulk of food provisioning for their partner and brood. Several authors have suggested that small males should be better parents because they are more efficient foragers (e.g. Andersson and Norberg 1981). This increased efficiency could result from greater agility owing to low wing loading, reduced energy consumption during flight, and/or lower requirements for self maintenance. Studies of Tengmalm's [Boreal] Owls (*Aegolius funereus*) and Eurasian Kestrels (*Falco tinnunculus*) have provided evidence that small males are indeed better at supplying prey (Hakkarainen and Korpimäki 1991, Hakkarainen et al. 1996). We found no relationship between male body size and breeding success in Great Skuas and Parasitic Jaegers in either of two years. If small males are better food providers in these species, we would expect male size to influence clutch volume and laying date, because females rely heavily on male courtship feeding in the two weeks before laying when egg formation takes place (Furness 1987, Catry and Furness 1997a). However, we found no relationship between male body size and clutch volume or timing of breeding, despite very large samples. Similarly, Newton (1988) failed to find an effect of male body size on any fitness components of European Sparrowhawks (*Accipiter nisus*), a species with particularly pronounced RSD. Again, we must be cautious, because a relationship between male size and breeding performance might be evident only in some years, e.g. when individuals are facing particular challenging environmental conditions.

Interspecific comparisons also refute the hypothesis that small male size has evolved for efficient foraging during breeding. Given that the proposed benefits of small size in males are related primarily to reduced wing loading (there-by increasing agility and reducing flight costs), we can predict that in species where breeding males do not forage or chase their prey on the wing, the selective advantage of reduced size would not exist, and therefore RSD should be reduced or absent altogether. Interspecific comparisons within the Stercorariinae suggest otherwise. The species with the largest degree of wing dimorphism is the Pomarine Jaeger (*Stercorarius pomarinus*), which specializes in preying on lemmings that are caught during patrolling flights or from the ground, often by digging open lemming burrows (Cramp and Simmons 1983, Furness 1987). From its foraging mode, we would expect Pomarine Jaegers to have one of the smallest dimorphism indices, yet this species shows one of the largest (Table 7). It is particularly interesting to compare Great Skuas and Brown Skuas (*Catharacta antarctica*), two species that are morphologically very similar, even though Great Skuas diverged from the remaining species at a relatively early stage in the evolution of the *Catharacta* (Cohen et al. 1997). Brown Skuas and Great Skuas show virtually the same degree of dimorphism despite strikingly different foraging techniques during the breeding season (Table 7). Brown Skuas, particularly the Tristan Skua (*Catharacta a. hamiltoni*), forage mainly by walking around their territories and scavenging or pouncing on prey, which consist mostly of procellariiforms that come ashore at night (Furness 1987, Young et al. 1988). By contrast, Great Skuas search for and catch food exclusively on the wing, mainly by splash-diving onto surface shoals or competing for discards behind fishing vessels, but also by kleptoparasitism and predation of seabirds (Furness 1987, Phillips et al. 1997). Across all species, no relationship seems to exist between foraging behavior and RSD in the Stercorariinae (Table 7). This contradicts the "small efficient male" hypothesis but fits well with behavioral hypotheses (see below) that state that morphology, not diet, is correlated with dimorphism in birds with a raptorial lifestyle (Smith 1982).

Does female dominance (or large RSD) improve breeding success?—Sex-role partitioning should be more efficient when females can readily force males into the role of food providers while preventing them from taking a greater role in incubation or brooding rearing (Smith 1982). In our study, the degree of dimorphism within pairs was not correlated with any breeding parameters except laying date in Parasitic Jaegers in one of two years. Thus, no clear support exists for this hypothesis, although it should be stressed that our tests are not very powerful because of the relatively small number of pairs in which both birds were measured.

In theory, intersexual competition for food on territories during the breeding season should select for a high degree of size dimorphism within pairs (e.g. Newton 1979, Andersson and Norberg 1981). If this hypothesis is correct, then RSD should be lower in skuas and jaegers that feed mostly outside of their breeding territories (e.g. Great Skua and South Polar Skua [*Catharacta maccormicki*]). However, RSD in these species is not particularly small relative to other skuas and jaegers (Table 7). At southern colonies, Parasitic Jaegers feed mainly by kleptoparasitism outside their breeding territories (Phillips et al. 1996b), but this is rare in the northern part of their range where most of the birds breed.

Is RSD related to intrasexual competition or pair formation?—If small males are more agile, then they should perform better aerial displays during courtship, which might facilitate the acquisition of mates. This hypothesis has been presented to explain RSD in some shorebirds and in raptors (Widén 1984, Jönsson 1987). Because large *Catharacta* skuas seldom perform aerial displays during courtship (Furness 1987), this hypothesis cannot apply to these birds.

Parasitic Jaegers mate assortatively by size, and the same might apply to Great Skuas, implying that small females avoid pairing with large males. This conforms with behavioral theories that propose that RSD evolved to facilitate pair formation. Female dominance is particularly important in species where aggressive and well-armed males could inflict injuries during the initial stages of pair formation (Smith 1982). This would tend to explain the large RSD in species that feed on relatively large and fast-moving prey (i.e. birds and mammals), because these species are better equipped to inflict serious injury (Smith 1982). However, studies of European Sparrowhawks (Newton 1983), American Kestrels (*Falco sparverius*; Bowman 1987, Bortolotti and Iko 1992), and Barn Owls (*Tyto alba*; Marti 1990) failed to find a correlation between the size of males and females in mated pairs. Clearly, the need exists for more studies of assortative mating by size in raptors, skuas, and jaegers.

If large RSD within pairs facilitates pair formation, then RSD should be correlated with the timing of breeding, at least in newly formed pairs. Because survival rates and mate fidelity are high in the species we studied, there were not enough new pairs to test this relationship. Including all pairs, no such effect was found in Great Skuas, but in one of two years, Parasitic Jaeger pairs with large RSD laid relatively early in the season. This is similar to Dunlins (*Calidris alpina*), a shorebird that displays RSD but that obviously has a non-raptorial lifestyle (Jönsson 1987).

Large female size could also result from intrasexual competition for mates, a hypothesis that also applies to raptors (Olsen and Olsen 1987). Female Great Skuas regularly engage in fights for males. In Great Skuas, and possibly in other species, such fights are resolved on the ground and sometimes cause fatal injuries (Catry et al. 1997). If large females have an advantage, then we would expect them to be paired with higher-quality males. This notion is supported by the fact that female size is positively correlated with male age. Newton (1988) found that large female European Sparrowhawks bred at a younger age than smaller females, a pattern that could also result from female-female competition for mates and/or territories. Large female Great Skuas paired with higher-quality males need not necessarily achieve higher breeding success because above a certain point, large size could becomes disadvantageous when performing breeding duties, even though it permits birds to compete for males.

It might be argued that if large females win intrasexual contests, they should also select small males (if one accepts that RSD facilitates pairing). However, large females may be able to easily assert dominance over any partner and therefore might not be constrained by male size in their choice of a mate. Accordinly, assortative mating by size simply could result from medium-sized or small females avoiding pairing with large males.

Conclusions.—Our study provides evidence against theories claiming that male and female body-size differences in skuas and jaegers evolved because of specialized roles during breeding. Large females were not more fecund, nor were they the main defenders of the nest. We found no evidence that small males were more efficient at foraging. In addition, interspecific comparisons did not support the idea that the degree of RSD is related to foraging behavior during the breeding season (as opposed to morphology), or that small male size evolved to reduce wing loading. The degree of dimorphism within pairs did not affect any breeding parameters. There was some indication that RSD is linked to sexual selection, because large females seemed to have an advantage in pairing with older males. Small males can also have an advantage in pairing if large males are rejected by small partners, as suggested by evidence of assortative mating by size in our study populations.

The origin and maintenance of RSD in birds (mostly predatory species) has been the subject of considerable recent debate. The question is far from settled, and little agreement exists regarding fundamental issues such as whether or not RSD in different families is a consequence of similar selective pressures. The problem is extremely complex, and our study does not provide any definitive answers. However, we believe that additional detailed field studies are necessary to elucidate the selective pressures that currently act to maintain RSD in natural populations.

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