The Auk 110(4):736–751, 1993

COMMUNICATIVE BEHAVIOR IN BREEDING OSPREYS (*PANDION HALIAETUS*): DESCRIPTION AND RELATIONSHIP OF SIGNALS TO LIFE HISTORY

VINCENT BRETAGNOLLE[1] AND JEAN-CLAUDE THIBAULT[2]

[1]*Centre d'Etudes Biologiques de Chizé, Beauvoir sur Niort, 79360, France; and*
[2]*Parc Naturel Régional de la Corse, BP 417, Ajaccio, Corse, 20184, France*

ABSTRACT.—The Osprey (*Pandion haliaetus*), although studied extensively, is relatively unknown with respect to its behavior, especially communication. We conducted a two-year study on a resident Osprey population in Corsica, and describe the communicative behavior of this species. The behavioral repertoire of Ospreys included 11 visual displays (resting, upright, alarm low and high, solicitation low and high, defense, protection, nest protecting, attack, and sky dance) and eight acoustic signals (alarm, solicitation low, high and very high, guard, excited, screaming, and copulation calls). The meaning of each of the displays and calls was inferred from the analysis of behavioral sequences. The communication system of the Osprey consisted of sexual behaviors (between partners), such as solicitation and sky dance, and agonistic behaviors (between breeders and nonbreeders), such as nest-protecting and defense postures. We also analyzed Osprey relationships with other species (including man), and found that there was a gradation within alarm displays and alarm calls according to stimulus distance. In the last section, we try to account for several peculiarities of Osprey behaviors, namely their complexity, the behavioral sexual dimorphism, and the importance of motivational displays. We suggest that all these characters may be related to the life-history traits shown by this species: semicoloniality, breeding strategy, and predation risk (on eggs and chicks). *Received 30 March 1992, accepted 25 November 1992.*

THE COMMUNICATIVE BEHAVIOR of many birds is relatively well known, and the relative completeness of our knowledge has permitted detailed comparative analysis (Tinbergen 1959, Johnsgard 1965, McKinney 1965, VanTets 1965, Kear 1970, Jouventin 1982, Kroodsma and Miller 1982, Hailman 1989). However, for some families and orders our knowledge is far from complete (Schleidt et al. 1984, Miller 1989). For example, the behavior, especially communication, of raptors has been virtually ignored (Newton 1979, Palmer 1988, Rosenfield and Bielefeldt 1991), even in such well-studied species as the Peregrine Falcon (*Falco peregrinus*; Ratcliffe 1980), the Golden Eagle (*Aquila chrysaetos*; Ellis 1979), and the Osprey (*Pandion haliaetus*). Two possible reasons for this may be that raptors are generally solitary birds, which is usually synonymous with depauperate behavioral repertoires, and are of large body size, meaning that their natural population densities are usually low, which reduces opportunities for observing social behavior (Brosset 1973).

There are, however, social (e.g. Harris' Hawk [*Parabuteo unicinctus*] and Galapagos Hawk [*Buteo galapagoensis*]; Faaborg et al. 1980, Faaborg and Bednarz 1990, Dawson and Mannan 1991) or colonial raptors. The Osprey exhibits coloniality in some local populations (Hagan and Walters 1990). For example, on Gardiner's Island (12 km^2), 300 pairs bred (Palmer 1988), with nests spaced no more than 50 m apart, and some as close as 10 m (cited in Cramp and Simmons 1980). However, though it is one of the most intensely studied raptor species, the Osprey's communicative behavior has not been fully documented. Illustrations of some displays can be found in Cramp and Simmons (1980), and sonagrams of three vocalizations were published by them and by Poole (1989a).

We describe the communication system of the Osprey and, thus, restrict our study to the displays (Moynihan 1955), including those that are signals and contain a message (see Smith 1977 and Beer 1982 for further details), and some elementary acts (e.g. copulation, fighting). Osprey communicative behavior was found to include 11 visual displays, most of which have

not previously been described, and eight acoustic signals. To understand the meaning of the displays, we quantified behavioral sequences in different contexts: sexual context between partners; agonistic context between breeders and conspecific intruders; and other contexts involving Ospreys and competitors or predators. In the last section, we discuss the significance of the behavioral repertoire of the Osprey with regard to its life-history strategy.

Materials and Methods

Corsica (42°N, 9°E) is a large western Mediterranean Island (8,722 km²; Fig. 1), where the Osprey population has been monitored since 1977 (Thibault and Patrimonio 1991). In 1990 and 1991, respectively, 16 and 19 pairs nested on the island, all on sea cliffs (Thibault and Bouvet 1983). Some birds (mainly males) are sedentary, while others are at least partial migrants (Thibault and Patrimonio 1989). Males reoccupy nest sites before females. Egg laying occurs in March and April, and fledging in June and July for the Corsican population (Fig. 1).

Detailed studies were made during 20–27 June 1990, 12–30 March 1991, and 8–16 June 1991 on 11 nests. Continuous observations (usually from 0800 to 1900) were carried out and included the prelaying, egg-laying, and the end of the chick-rearing periods (Fig. 1). Observations were made either 300 m from the nest with a telescope (20–70×), or from a blind 40 to 80 m from nest. Behaviors were recorded continuously on data sheets (continuous focal-animal sampling; Altmann 1974) and their context noted (e.g. activity or display given by partner, another Osprey, or intruder). Sex was determined on the basis of plumage pattern (e.g. Cramp and Simmons 1980). Where a description exists in the literature of a display (or a call), we followed the terminology employed by previous authors.

Ospreys were recorded with an Uher 4400 tape recorder and a Seinnheiser MKH 815 unidirectional microphone at 19.05 cm/s on AGFA PE43 tape. We recorded 250 calls from nine pairs (1990 and 1991 combined). Calls were analyzed on an Amiga microcomputer using an analytic package that performs a fast Fourier transform (sampling rate 6,512 Hz; step size 256 points; Richard 1991). Sonagrams were printed with a Kay 6061B Sonagraph.

Both within- and between-individual transitions of behaviors were studied through the use of contingency tables (matrix of transition; see Standen 1980, Slater 1983). A first set of matrices was constructed in which visual and acoustic displays were analyzed as responses to different contexts (i.e. behavior of partner or presence of intruder [Osprey, other bird, man, etc.]). In a second matrix, visual displays were analyzed (in females only) in terms of successive acts. Behaviors were tabulated as stimulus (or preceding) behaviors in the columns and response (or following) behaviors in the rows. The frequency with which a stimulus behavior was followed by a response behavior was entered in the table (diagonal values, implying a behavior following itself, were excluded from intraindividual transition matrix; Standen 1980, Slater 1983). For a behavior to be defined as following a stimulus, it had to be observed within 15 s of the latter. Contingency tables were analyzed first with an overall chi-square test (lumping data if frequencies were too low) for significance (i.e. nonindependence), and second with chi-square tests performed on partitioned 2 × 2 contingency tables to search for more or less than expected degrees of association between behaviors (for a similar procedure, see Standen 1980). However, in view of the number of tests that were performed, *P*-values were considered significant if less than 0.01 when fewer than 20 tests were involved, or if less than 0.001 with 20 or more.

Results

Description of visual displays.—Elementary acts included typical bird activities, such as yawning, preening, copulation (described in detail by Cramp and Simmons 1980), fighting (overt attack at nest), and resting. This latter activity constituted the baseline activity of Ospreys, to which all other displays subsequently were compared. In adults at least, resting (Figs. 2a, b, and c) showed slight sexual dimorphism (Figs. 2a and b); males typically are more upright than females, with more widely opened wings.

The upright display was distinguished from resting mainly by the more vertical general body axis, and the position of the neck (Figs. 2d and e); wings were held slightly opened. In a highly motivated expression of this display, observed twice, a male showed extensively erected crest feathers.

The alarm display (Figs. 2e and f) involved a marked extension of the neck, which was further crooked (unlike in upright display). We recognized two variants (subsequently analyzed as two different signals) of this display according to bird motivation (see below).

The solicitation display was given only by females (Figs. 3a and b) and by chicks nearing fledging. Two types of this display occurred (subsequently analyzed as two signals), according to bird motivation (Figs. 3a and b). In both, the body axis was horizontal, the crest feathers were slightly erected, and the wings were held close to the body.

The protection display (Fig. 3c) and defense

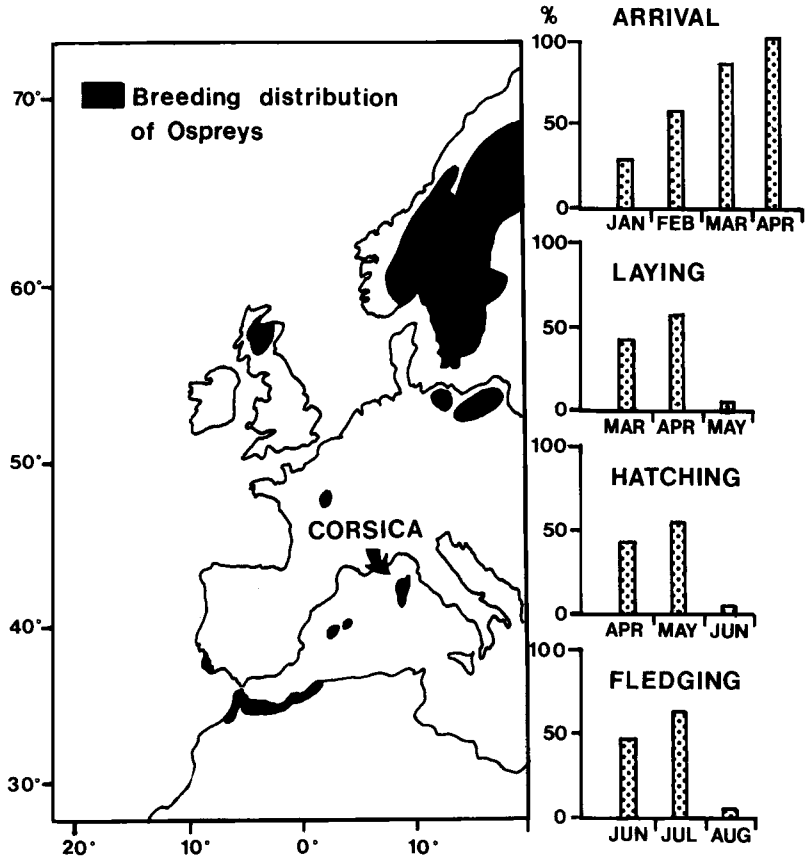

Fig. 1. Study area and breeding phenology of Ospreys. Breeding distribution of Ospreys in western Palearctic (modified from Cramp and Simmons 1980, Poole 1989a), showing location of Corsica. Graphs on right indicate chronology of breeding of resident Ospreys in Corsica.

display (Figs. 3e and f; also illustrated in Cramp and Simmons 1980) are two rather similar displays, distinguished by wing position in relation to the body. In protection display, shoulder and carpal joints were close to the body, and the body axis was usually more or less horizontal; in the defense display, the wings were mostly opened, and the carpal joint was close, or lying on the ground. In a highly motivated version of this display, the bird could move to a more horizontal position, with the tail raised and contracted (Fig. 3d).

The nest-protecting display (Cramp and Simmons 1980) was characterized by wing shaking, a fanned tail, and a horizontal position (Fig. 3d).

We observed only one type of flight display, the sky-dance display (for extensive description, see Cramp and Simmons 1980). This behavior was only recorded in males during our study, although females are apparently known to perform it (Cramp and Simmons 1980). We did not see the "hovering display" (Cramp and Simmons 1980, Poole 1989a) and suspect it is only a variant of sky-dance display. Thus, the visual repertoire of the Osprey included nine different signals, and several elementary acts that shall be included here (i.e. copulation, attack and resting).

Description of calls.—Some previous call descriptions are to be found in Cramp and Simmons (1980) and Poole (1989a:113). The alarm call (Fig. 4a) has been described in both references cited above, and shows a clear sexual dimorphism as illustrated in Poole (1989a:113). The solicitation call (Figs. 4b, c, and d) was only given by females and has three versions that have not previously been noted in the literature. The three differed in temporal and frequency parameters, but represent a continuum, as a female usually gave them successively ac-

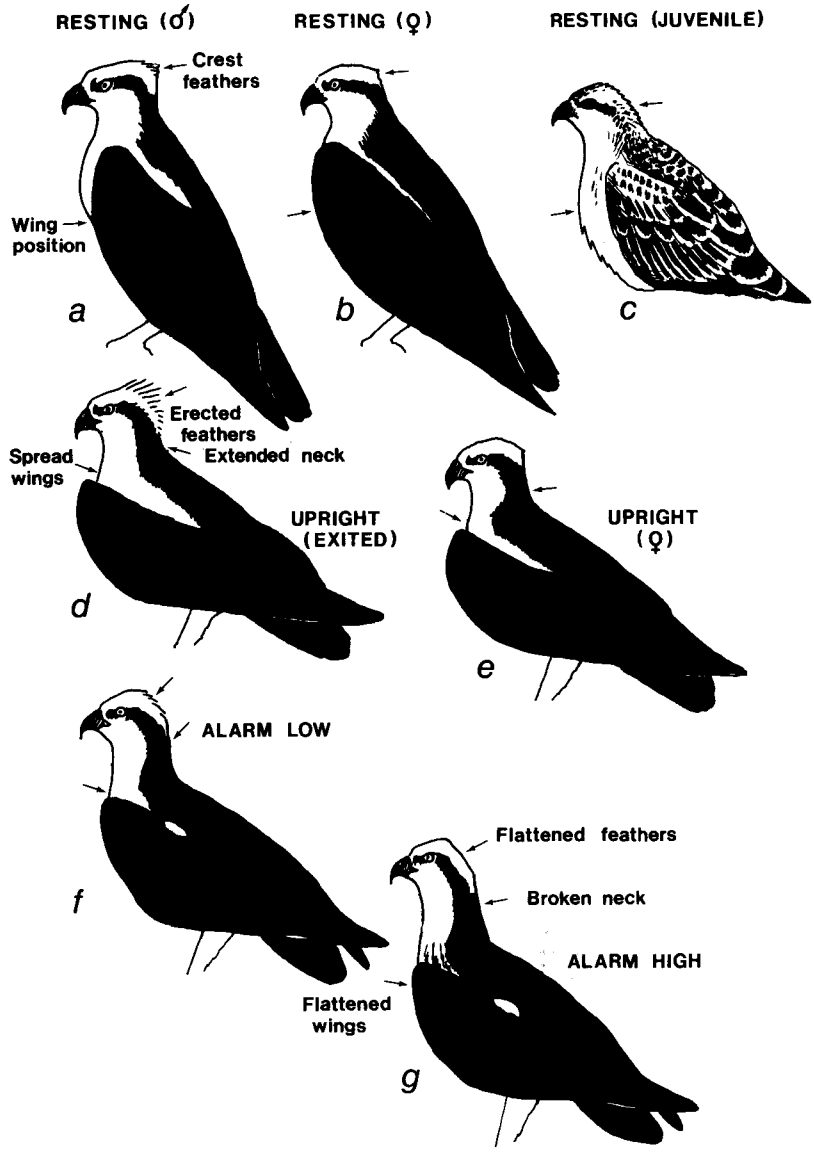

Fig. 2. Visual displays of male, female, and juvenile Osprey. Name of display given in capital letters. Arrows indicate important features of body that distinguish different behaviors (e.g. neck position, wing position, etc.).

cording to her motivation. The screaming call (following Henny in Palmer 1988) was given by both sexes (Figs. 4e and f) and usually in flight (see below). The guard call (following Poole 1989a:113) and the excited call were also given by birds of both sexes (Figs. 4g and h). The latter has not been described (although a sonagram is included in Poole 1989a:113); it always followed the guard call. Other previously undescribed calls include a copulation call (not illustrated) and different calls of the chicks. Very young chicks (under two weeks) gave a version of the guard call when fed (Fig. 4i). When older, they begged for food in the same way as the female (Fig. 4j). At a later stage, when exercising their wings, young sometimes gave the screaming call.

Associations between calls and visual displays.— As shown in Table 1, there was no strict concordance between vocalizations and visual dis-

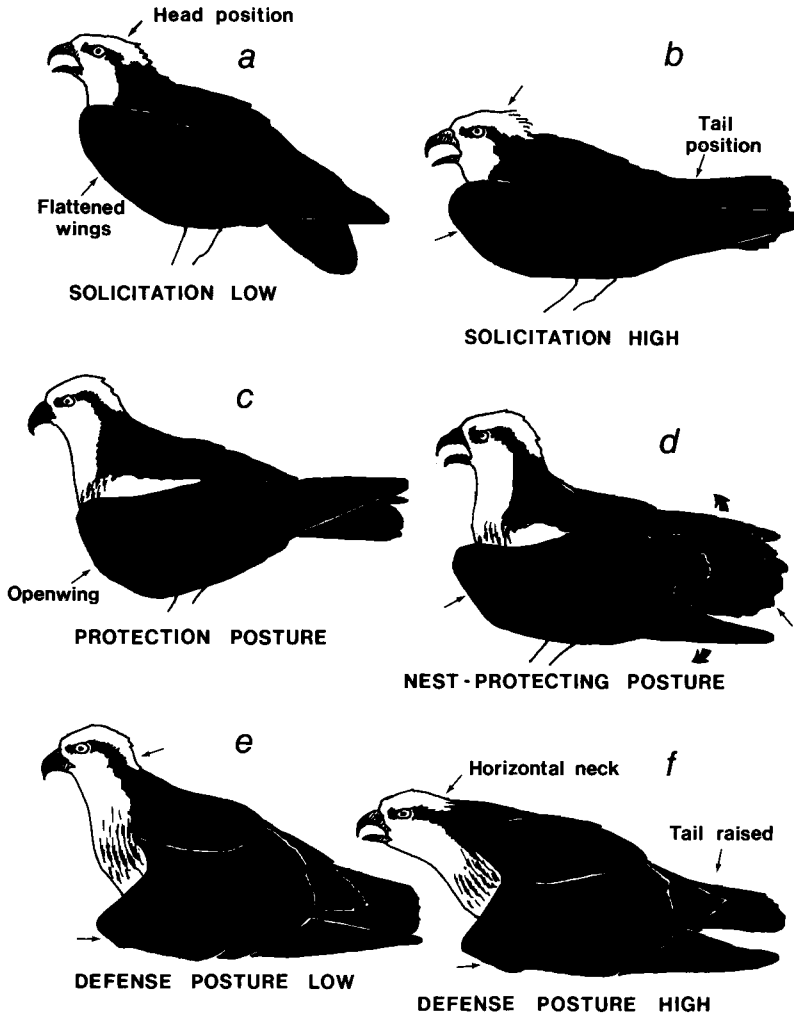

Fig. 3. Visual displays of Ospreys. Arrows indicate important features of body that distinguish different behaviors (e.g. neck position, wing position, etc.). Large arrow indicates wing movement in nest-protecting display.

plays, except for the screaming and solicitation calls, which were given respectively in association with flying and solicitation display. Other calls, although usually loosely associated with one particular display (e.g. defense with the guard call; Table 1), were also associated with others. Some displays were not associated with vocalizations (alarm display), while others were systematically accompanied by calls (solicitation, nest protecting; Table 1). Lastly, there was a parallel gradation between some calls and some displays, namely from guard to excited through screaming calls, and upright, protection, defense, and nest-protecting displays ($X^2 = 28.1$, df = 6, $P < 0.001$; Table 1).

Behavioral differences between sexes.—There was no obvious sex difference in the rate of emission of visual or acoustic signals (5.28 vs. 6.06 visual displays, and 5.38 vs. 6.42 acoustic signals/h at nest for females and males, respectively; Table 2). However, we found qualitative and quantitative sexual dimorphism of visual displays and calls (Table 2). In the case of males, 78% of all instances of behavior noted were occurrences of upright, defense, and sky dance, while alarm, solicitation, and nest protecting accounted for 72% of female behaviors (Table 2). With regard to calls, screaming and guard calls were often uttered by males (65%), while females uttered mainly solicitation calls (55%). Moreover,

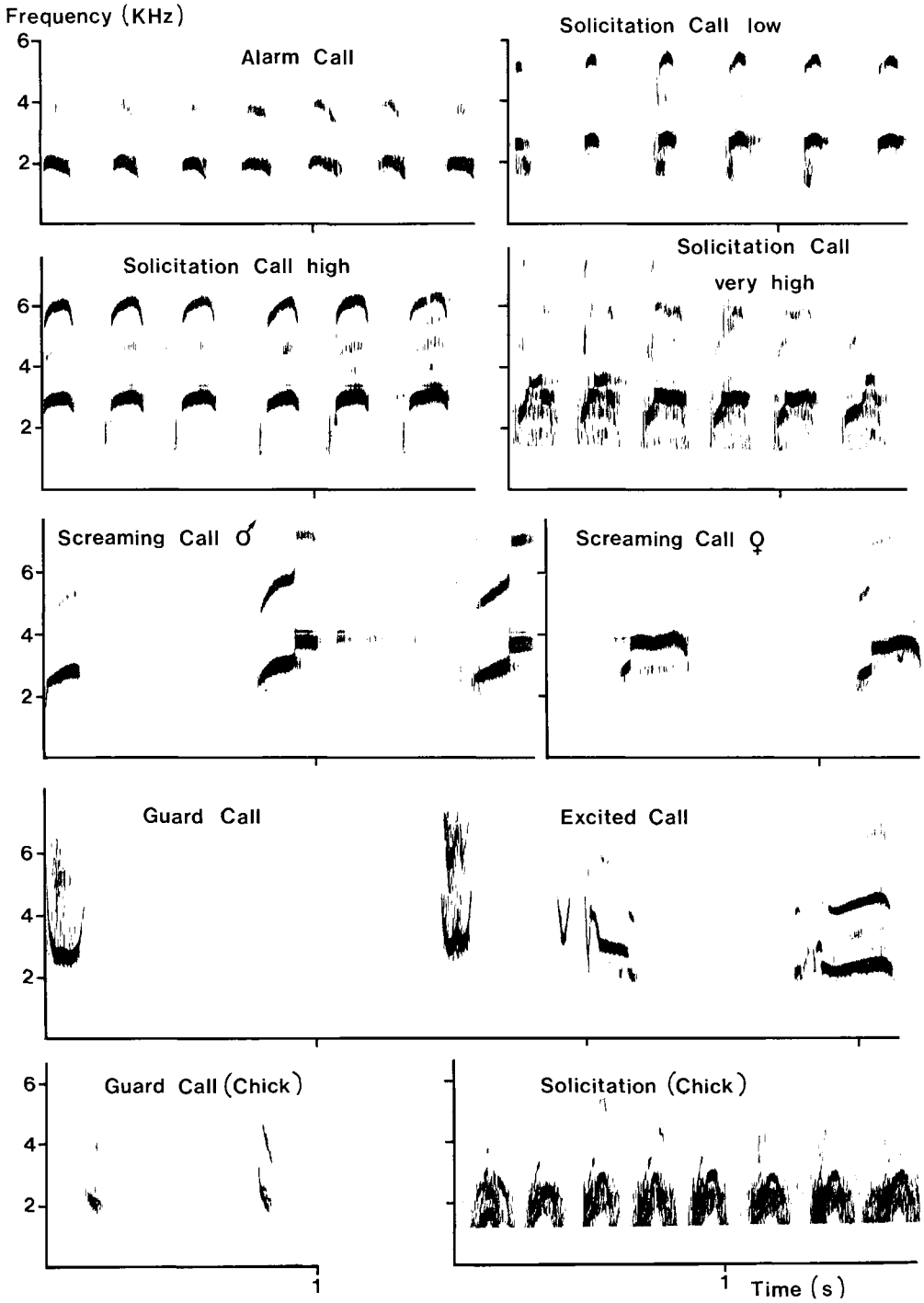

Fig. 4. Calls of male, female, and juvenile (chick stage) Ospreys (time in seconds; frequency in kilohertz).

TABLE 1. Frequency of associations between visual displays (columns), and acoustic signals (rows).

Acoustic signal	Visual display										
	Flight	Alight	Resting	Alarm	Upright	Solicitation	Feeding	Protection	Defense	Nest protecting	Totals
Alarm call	42	16	27	3	3	0	7	0	0	3	101
Solicitation											
Low	0	0	37	2	7	18	14	0	0	0	78
High	0	1	27	0	3	36	18	0	1	1	87
Very high	0	0	7	0	0	17	8	4	5	2	43
Screaming call	34	0	0	0	0	0	0	7	0	14	55
Guard call	18	21	2	0	12	0	0	9	15	11	88
Excited call	4	2	0	1	0	0	0	5	2	11	25
Totals (with calls)	98	40	100	6	25	71	47	25	23	42	477
Totals (without calls[a])	—	38	—	32	13	0	—	23	27	24	—
Percent (without calls)	—	48	—	84	34	0	—	48	50	32	—

[a] Continuous activities (e.g. flying) not considered.

on a quantitative basis, significant differences in frequency of emission occurred in most displays (13 of 17; Table 2).

Influence of context on incidences of displays.— We first analyzed the sexual behavior of the pair (i.e. male behavior being taken as a stimulus possibly eliciting a response from female). An overall test of significance (data from Table 3, regrouping low and high versions within alarm and solicitation, excluding "take off" due to sample size; $X^2 = 225$; df = 32, $P < 0.0001$) indicated that male behavior had a strong influence on female behavior. Predominant female visual displays were related to alarm and solicitation activities (Table 3), which accounted for up to 61.4% of displays. This was also clear when only those associations that occurred more than would be expected (at $P < 0.001$) by chance were considered (Table 3). Male behavior induced two types of responses by females (see Fig. 5). First, the presence of the male, whether flying, being at the nest, or close to the nest, significantly elicited solicitation (low or high). Female behavior differed whether the male carried a fish (solicitation high), nothing (solicitation low), or a branch (resting; i.e. no response). Second, although this was less obvious, males (e.g. when landing at nest) seem to elicit from females behavior associated with being alert, as the latter showed alarm and upright (Table 3 and Fig. 5). Similar results were obtained for calls, with solicitation calls accounting for 96% of the calls emitted by females (Table 3) in response to male behavior.

We also analyzed the behavior of the breeders facing the intrusion of another Osprey (sex undefined) close to the nest (Table 4). In that context, breeders showed three types of displays (see Fig. 6): (1) nest protecting, the commonest visual display; (2) taking off; and (3) guard, screaming, and excited calls (Table 4). Further-

TABLE 2. Comparisons (chi-square tests) between sexes of frequencies and percentages of displays and calls.

Display	Given by[a]		P[b]
	Female (%)	Male (%)	
Upright	26 (7.0)	12 (16.7)	<0.01
Alarm			
Low	53 (14.4)	3 (4.1)	ns
High	46 (12.5)	3 (4.1)	ns
Solicitation			
Low	50 (13.6)	0 (0.0)	<0.001
High	66 (17.9)	0 (0.0)	<0.001
Protection	35 (9.5)	6 (8.3)	ns
Defense	33 (8.9)	17 (23.6)	<0.001
Nest-protecting	49 (13.3)	4 (5.6)	ns
Attack	11 (3.0)	0 (0.0)	ns
Sky-dance	0 (0.0)	27 (37.5)	<0.001
Alarm call	81 (21.5)	16 (21.1)	ns
Solicitation call			
Low	65 (17.3)	0 (0.0)	<0.001
High	92 (24.5)	0 (0.0)	<0.001
Very high	49 (13.0)	0 (0.0)	<0.001
Screaming call	23 (6.1)	16 (21.1)	<0.001
Guard call	49 (13.0)	33 (43.4)	<0.001
Excited call	17 (4.5)	11 (14.5)	<0.001

[a] Totals for females and males, respectively, during 1990 and 1991; acoustic signals, 376 and 76; visual displays, 369 and 72; times of observation, 4,192 and 710 min.

[b] For these analyses, ns used for $P > 0.01$.

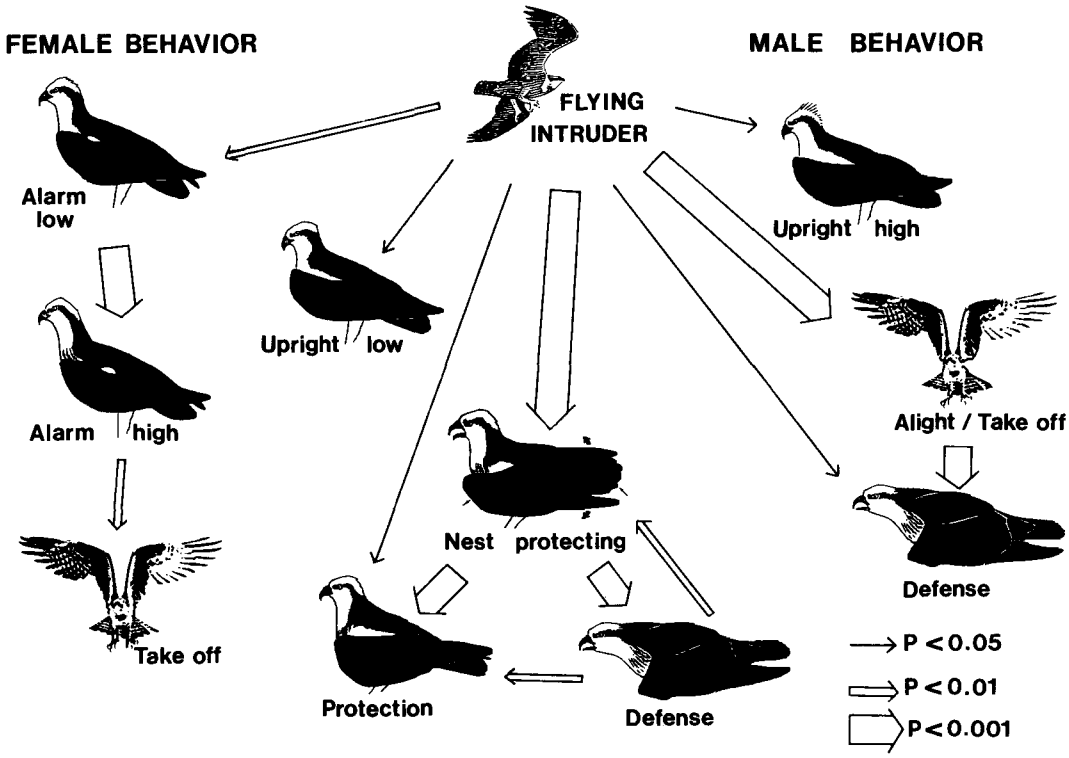

Fig. 5. Summary of visual displays related to type of stimulus. Female behavior elicited by male behavior. Arrow thickness indicates probability level (data from Tables 4 and 6).

more, although sample size was low for males, significant sexual differences were found. Nest protecting was almost exclusively given by females, whereas movements were typical male responses; males alighted if flying over the nest, or took off if at the nest (Fig. 6). Other behaviors were rarely shown. Conversely, no significant sexual differences were found with regard to calls.

We also analyzed the behavior of male and female Ospreys when a potential predator/competitor (i.e. something other than an Osprey) approached the nest (Table 5). In each case, whether the "intruder" was a boat, gull, raven, or raptor, the display changed as the distance between the bird and the stimulus decreased (Table 5). In the case of a boat, the sample size was large enough to allow statistical analysis. At 500 m or more, this stimulus elicited no response in 89% of cases. At less than 250 m, both alarm versions accounted for 57% of responses. And at less than 100 m females took off in 61% of cases and males performed the sky-dance display in 45% of cases. This gradation in display use was highly significant ($X^2 = 85.7$, df = 10, $P < 0.001$). Similar gradations were observed for other stimuli (Table 5). The alarm call on the other hand was mainly associated with human and boat presence close to the Ospreys (Table 5).

Succession of visual displays.—To evaluate sequences of visual displays, we considered those of females alone given the small sample sizes for males, and the calls for both sexes. Overall tests for significance revealed that the following behaviors did not occur at random (Table 6; lumping low and high versions of alarm and solicitation, and defense, protection, and nest protecting in stimulus behavior; $X^2 = 435$, df = 32, $P < 0.0001$). Baseline activity (resting) was significantly followed by upright, alarm-low, and solicitation-low displays. This indicated presumably that these displays conveyed the lowest degree of motivation from the female. A next step in motivational intensity was reflected by solicitation high and alarm high, which significantly followed solicitation low and alarm low, respectively (Table 6). The three

TABLE 3. Behavior elicited in female as response to stimulus from male[a].

Behavior of female (response)	Behavior of male (stimulus)						
	Flying	Alighting with branch	Alighting with fish	Alighting	Taking off	At nest	Total
Visual displays							
Resting	3	5	0, −***	6	27, +***	0, −***	41
Upright	3	1	2	5	2	4	17
Alarm low	7	3	0	7	4	4	25
Alarm high	2	0	1	4	4	0	11
Solicitation low	22, +***	0	7	4	0	19	52
Solicitation high	10	0	23, +***	0, −***	0, −***	33, +***	66
Protection	1	0	1	1	0	3	6
Defense	0	0	2	0	0	7	9
Nest protecting	1	0	0	0	0	0	1
Copulation	8	3	0	2	0	6	19
Take off	0	0	1	0	0	0	1
Alight	0	0	9, +***	0	0	0	9
Total	57	12	46	29	37	76	257
Calls							
Solicitation call low	6	0	6, −***	16, +***	1	18	47
Solicitation call high	10	0	31, +***	0, −***	0	20	61
Solicitation call very high	3	0	22, +***	0	0	5	30
Guard call	3	0	2	0	0	0	5
Screaming call	1	0	0	0	0	0	1
Total	23	0	61	16	1	43	144

[a] For each cell of table, 2 × 2 chi-square test used for comparing observed and expected frequencies. For example, when an association occurred significantly more than expected, a "+" follows the frequency (or a "−" for a negative association). Only values with $P < 0.001$ (***) judged significant.

TABLE 4. Comparison (chi-square and Fishers's exact tests) of frequencies of response of female and male Ospreys at their nest to intrusion of another Osprey close to eyrie (<200 m). Only values with $P < 0.01$ judged significant.

Behavior	Behavior of			
	Female	Male	Total	*P*
Visual displays				
Resting	7	4	11	ns
Upright	7	4	11	ns
Alarm	12	0	12	ns
Protection	11	0	11	ns
Defense	10	5	15	ns
Nest protecting	48	3	51	0.0004
Take off	13	11	24	0.01
Alight	5	8	13	0.002
Total	113	35	146	
Calls				
Alarm	6	0	6	ns
Solicitation	2	0	2	ns
Guard	27	14	41	ns
Screaming	19	6	25	ns
Excited	21	6	27	ns
Total	75	26	101	

remaining displays—nest protecting, defense, and protection—showed complex interactions and were more or less related to each other. Defense and protection displays followed solicitation high, and occurred in sequence; when the male brought a fish, the female showed solicitation high until the male gave the fish, when females showed defense and/or protection display (Fig. 5). In these types of sequences, nest protecting was never observed. In a different context, when another Osprey flew over the nest, nest protecting occurred after upright display, and followed or preceded (equally) defense and/or protection displays (Table 6 and Fig. 6).

DISCUSSION

Our interest is in accounting for the meaning and function of each visual and vocal signal of the Osprey. Meanings can be deduced from both the context in which the display occurred, and its effects on the receiver bird (for general discussion and definitions of signal, message, and meaning, see Smith 1977). After addressing these

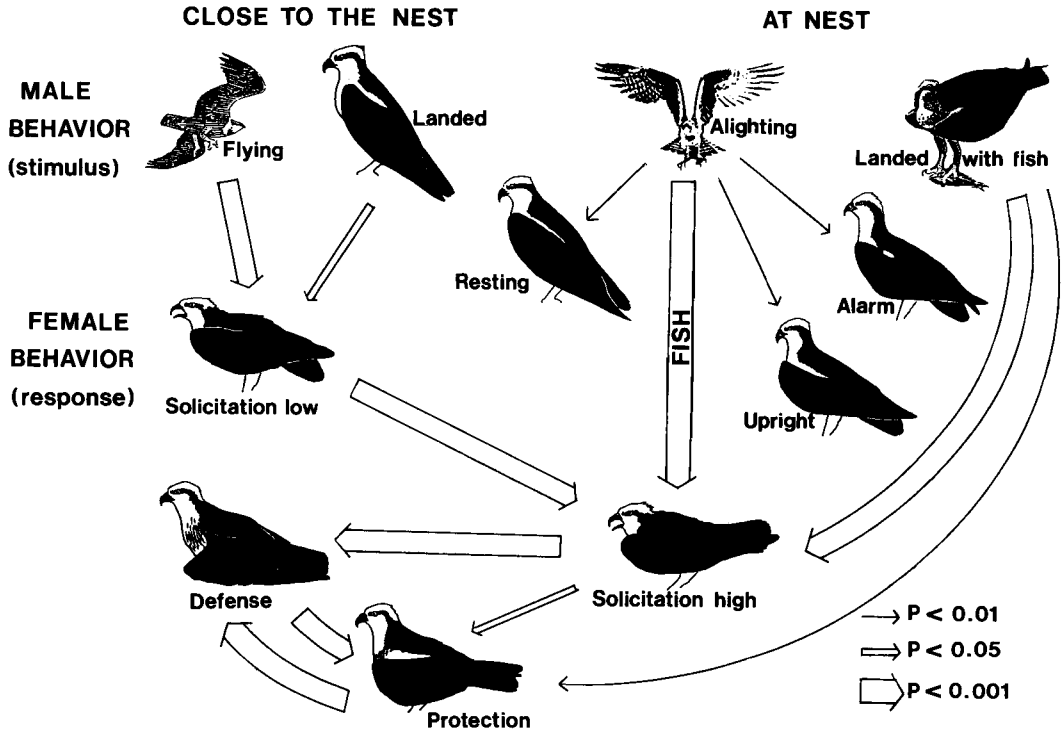

Fig. 6. Summary of visual displays given by male and female Ospreys when an Osprey intruder approached nest (data from Tables 5 and 6). Arrow thickness indicates probability level (data from Tables 4 and 6).

matters, we discuss the biological significance of behaviors with regard to the life history of the Osprey, and emphasize how behavioral and ecological life-history traits are connected to each other.

Osprey coloration.—Although coloration has been seldom discussed as a behavioral element in repertoires, it obviously can function in communicative behavior (Mock 1980, Jouventin 1982, Zahavi 1988). The coloration of the Osprey is interesting as it is simple and of high contrast. Osprey flight coloration undoubtedly is related to its fishing behavior (for a review on fish-eating seabirds, see Cairns 1986); complex underwing coloration might enhance fish capture efficiency through a disruptive effect (Wilson et al. 1988). We suggest that the coloration of Ospreys when they are perched may play a part in communicative behavior (see also Bretagnolle et al. 1994). The black-and-white contrast may exaggerate some of the visual displays. It outlines the neck form and shape in those displays that indicate an increased level of attention (relevant for alarm and upright displays compared to resting). Also, the white border on the back outlines the position of the wings (relevant for defense, protection, and nest-protecting displays). Wing position is an agonistic indicator (see below). These findings are supported by comparison of male, female, and juvenile coloration. The contrast is reduced in females compared to males (mainly by neck position in resting and upright, and dark breast coloration). Moreover, when females beg for food (solicitation display), they substantially reduce this contrast in both neck (head is kept hunched) and back (wings kept close to body). Conversely, the amount of white shown by the males on their backs when perched appears greater than in females (Fig. 2). Such contrast is absent from fledgling birds, where white is replaced by cream color, and black by rufous or brown (Fig. 2).

Osprey mating.—Some visual displays are mainly found in heterosexual behavior (i.e. involving partners). For females, these include solicitation and to a lesser extent alarm and upright, while sky dance was the predominant

TABLE 5. Frequency of displays (visual and acoustic) used by breeding Ospreys when an intruder approached.

Behavior	Boat			Man	Gull			Raven		Raptor		Total
	<500 m	<250 m	<100 m	<100 m	<150 m	<100 m	<50 m	<100 m	<75 m	<50 m	<200 m	<100 m	
Resting[a]	32	13	0	0	15	13	10	3	0	0	11	3	100
Alarm low	3	9	0	0	1	4	9	3	0	0	0	1	30
Alarm high	0	11	11	0	0	1	3	0	2	2	1	0	31
Take off	0	2	17	24	0	0	2	0	0	3	0	7	55
Sky dance[b]	0	0	9	9	0	0	0	0	0	0	0	0	18
Total visual displays	35	35	37	33	16	18	24	6	2	5	12	11	234
Alarm call	0	4	35	64	0	0	7	0	0	0	0	0	110

[a] Resting is baseline activity, and its occurrence indicates that bird did not respond to stimulus.
[b] Only observed in males.

male activity (Table 3). Thus, it is expected that the function of those displays is related to mating and/or pair-bond maintenance.

Male mating behavior included mainly the sky dance (see also Poole 1989a), which is a typical raptor mating display found in many other species (Tubbs 1974, Newton 1979, Watson 1977, Gargett 1990). It is highly conspicuous and likely to be directed towards both females (advertising) and males (exclusion; Poole 1989a). Mating is fairly rapid in the Osprey (Green 1976, Jamieson et al. 1982, Henny in Palmer 1988, Poole 1989a). The sky dance, known to be given frequently by Ospreys (Cramp and Simmons 1980, Poole 1989a), may play a part in this rapid mating. However, the sky dance was a relatively rare display in Corsica (pers. obs.), and we suggest that rapid mating might be a consequence mainly of mate and site fidelity from year to year in this species (Jamieson et al. 1982, Poole 1989a, Postupalsky 1989, Thibault and Patrimonio 1991). Moreover, Corsican Ospreys are resident, which may also facilitate pairing. Though Greene (1987) suggested that the sky dance is used by males to indicate successful fishing to other males of the colony (following information-center theory; Ward and Zahavi 1973), we suggest that his sample sizes were limited and do not exclude the possibility that the sky dance is primarily a sexual behavior.

Female sexual behavior included solicitation, although it is not strictly related to mating. Courtship feeding is of major importance in the Osprey, especially for female productivity (Birkhead and Lessel 1988, Poole 1989a). Thus, it is not surprising that some displays are devoted to solicitation for fish. Moreover, feeding by male Osprey continues throughout breeding and, therefore, solicitation may be interpreted as having a proximate (to obtain food) and an ultimate (pair-bond reinforcement) function. Other displays (alarm and upright) are not related to mating, and appear in heterosexual behavior as a by-product of antagonistic relationships (see below).

Osprey agonistic behavior.—The agonistic nature of nest-protecting, protection, and defense displays is revealed by their occurrence in aggressive contexts: when an intruder flies over the nest (especially for nest protecting; Table 4); or when there is a dispute between the partners for a fish (defense and protection displays; Table 6). Nest protecting is a display almost exclusively given by the female (Tables 2 and

4) and directed toward flying birds (Table 4). Wing shaking in the nest-protecting display, clearly emphasized by the white border of the back (Fig. 4), is especially visible from above. Nest protecting is highly agonistic, as it is quite often followed by direct attack if the intruder has landed (Table 6). Conversely, when the intruder leaves, nest protecting is followed by defense and/or protection (Table 6). This suggests that defense and protection have a lower agonistic content, and they are in fact less likely to be directed toward an intruder (Table 4).

Defense is a very typical raptor display, and can be regarded as a food-defense posture that generally occurs just after the kill. It appeared in a slightly different context in the Osprey (i.e. when the female obtained a fish from the male and wanted to keep it from him). We also found another context in which male Ospreys exhibited defense: at the beginning of the breeding season, and typically during the copulation period, sighting an Osprey intruder can induce a male to alight and then to show defense display (Table 4). In this context, we suggest that the male tries to protect his female from extrapair copulation (Møller 1987, Birkhead and Lessel 1988) as he would protect a prey item.

The distinction between defense and protection is slight, and the latter might be an attenuated version of defense. Protection is rarely given by males (Table 3); however, protection often follows a defense display (Table 7) and is restricted to the fish-delivery context (which is not the case for the defense display). Protection, therefore, might be a version of the defense display as expressed in a sexual context.

Motivational signals in Ospreys.—Two visual displays, alarm and upright, direct a message to any bird, whether partner, chick, or conspecific, and occur in all contexts. Both are frequently given by the female (Tables 2, 4, 5, and 6), but alarm was seen only rarely in males. Alarm display was mainly given in response to a potential danger (Table 5); during the brood rearing period, it was directed toward chicks (in order to alert them), but it also occurred frequently in March when no chicks were present (pers. obs.). Upright also occurred in a similar context, and probably signifies an increased level of attention compared to resting (Tables 3 and 4). Both upright and alarm can be followed by almost any behavior (Table 6). We suggest that they are indicators of bird motivation.

The sky dance was regularly observed in males carrying fish when human observers were at the nest (i.e. for chick banding). We suggest that, in this context, the sky dance is a displacement activity (for similar observations, see Poole 1989a).

Apart from the alarm call (see below), we believe that calls do not act as signals by themselves, but indicate the degree of motivation of the emitter bird. First, calls nearly always accompanied visual displays and, therefore, were rarely uttered alone (Table 1). Second, calls were not associated with any specific display (Table 1). Third, there was no significant difference between male and female calls when an intruder flies over the nest (Table 4), whereas sex-biased responses occurred with visual displays. Only one call (solicitation) appeared in heterosexual context (Table 5), whereas other calls were mainly agonistic (Table 4). Moreover, these latter calls (guard, screaming, and excited) parallel the gradually increasing aggressivity of visual displays (upright, defense, protection, and nest protecting; Table 1). That calls underline emitter-bird motivation is also supported by the fact that some calls can appear in highly different contexts. For example, the screaming call appears in both sexual behavior (sky dance) and when the female is very frightened (see also Poole 1989a). The alarm call is the only call that conveys a signal exclusive of visual displays; it is mainly given by the female to alert the chicks that a potential danger approaches (Table 5). Thus, in 68% of cases ($n = 59$) that the female emitted the call, the chicks flattened themselves in the nest, increasing the effectiveness of their camouflage.

Osprey life history and biological significance of behaviors.—Nearly all raptors are sexually dimorphic (Newton 1979, Mueller and Meyer 1985, Mueller 1990), and the Osprey is no exception. Thus, it is not surprising that there is also sexual difference in communicative behavior of raptors, although this latter point, poorly documented, has mainly been discussed in terms of nest defense (Mueller and Meyer 1985, Andersson and Wiklund 1987). Behavioral differences between male and female Ospreys are found in: (1) the number of displays (some visual signals and calls are given by only one sex); (2) the form and structure of the display (vocal sexual dimorphism, sexual asymmetry in neck and head position); and (3) the meaning of some displays (e.g. screaming call). Ospreys show ex-

TABLE 6. Transition matrix for intraindividual progression (female only) of visual displays. Cell numbers represent frequencies of associations between (preceding) and second (following) behavior; a behavior cannot follow itself (i.e. diagonals excluded)[a].

Second behavior	First behavior			
	No display	Alarm		Upright
		Low	High	
Upright	18, +***	1	1	—
Alarm low	20, +***	—	0	1
Alarm high	9	22, +***	—	0
Solicitation low	39, +***	6	0	5
Solicitation high	4, −***	1	0	7
Defense	0, −***	0	1	5
Protection	5	0	1	6
Nest protecting	7	1	1	11, +***
Take off	17	1	27, +***	0
Attack	0	0	0	0
Total	119	32	31	35

[a] For each cell, a 2 × 2 chi-square test used for comparing observed and expected frequencies. For example, when an association occurred significantly more than expected, a "+" follows frequency (or a "−" for a negative association). Only values with $P < 0.001$ (***) judged significant.

treme role partitioning between the sexes. The male provides all of the food for both female and young (99% of fish are provided by male; Stinson et al. 1988, see also Jamieson et al. 1982), from the arrival on the breeding site until the departure of the juveniles (Green 1976, Poole 1989a). Conversely, the female Osprey stays at the nest for more than five months. We suggest that both female and male repertoires result from, and reflect, this difference. For the female, two activities are of major importance: food solicitation from the male; and nest defense against Osprey intruders (Green 1976, Poole 1989a, Hagan and Walters 1990) and predators (Stinson et al. 1988, Poole 1989a). With respect to food provisioning, females spend most of their time (frequency of occurrence of displays) in these activities, and the motivational state of the female (an important characteristic of food begging) is communicated by the two versions of solicitation display and three calls. Female nest defense is achieved through a ritualized display—nest protecting. Males, however, must provide nourishment for the entire family and leave the female for long periods of time. Ospreys are also semicolonial breeders and, thus, there is a high rate of potential conflicts with Osprey intruders. Since males cannot defend the nest and their mate all of the time, the male Ospreys have repertoires with very conspicuous (e.g. sky dance) and agonistic (e.g. defense) displays, in order especially to avoid extrapair copulation (Møller 1987, Birkhead and Lessel 1988). Therefore, we conclude that the sexual dimorphism in repertoires is originated in this wide sexual asymmetry of life histories.

Most raptor species defend feeding territories (Newton 1979), but the Osprey does not, especially in coastal areas (Greene and Freedman 1986; pers. obs.). Moreover, some Osprey populations (although not at present in Corsica) breed in loose colonies (references in Cramp and Simmons 1980, Palmer 1988, Poole 1989a, b, Hagan and Walters 1990). The absence of feeding territory may be related to diet, as fish are a spatiotemporally unpredictable resource (Poole 1989b, Edwards 1989). Recently, Greene (1987) showed that Osprey colonies may act as information centers, but this is not a general rule (Hagan and Walters 1990). Whether coloniality in the Osprey results from trophic or social factors (see Hagan and Walters 1990), we suggest that it has led to a complex repertoire with many ritualized displays. This may have been favored by a high potential rate of contact between individuals (e.g. Bretagnolle 1988, Hagan and Walters 1990). In Corsica, the frequency of intruder visits could reach 12 per day during the study period (up to 5/h), although landing of the intruder on another pair's nest is exceptional, and direct attack is even more rare. This may be a consequence of the well-developed social communication system, which includes several agonistic displays with increasing motivation. We suggest that both a large diversity and a specialization (ritualization) of displays are adaptive responses to semicoloniality and lack of feeding territories in the Osprey.

TABLE 6. Extended.

First behavior					
Solicitation					
Low	High	Defense	Protection	Nest protecting	Total
2	1	1	0	1	25
0	0	0	0	0	21
0	0	0	0	1	32
—	0	0	0	1	51
54, +***	—	0	0	0	66
0	14, +***	—	1	9, +***	30
0	8, +***	12, +***	—	13, +***	45
2	0	7, +***	11, +***	—	40
8	0	0	0	0	53
0	0	0	0	11, +***	11
66	23	20	12	36	374

Ospreys breed on very exposed (Poole 1989a) and large nests (up to 3 m in diameter; De-Naurois 1987). Osprey nests tend to be as inaccessible as possible, a response to terrestrial predation risk (see Poole 1989a), and the exposed placement of the nest might be a response to the Osprey's relative lack of flying agility (Saïller 1977). However, nests are still accessible to birds (e.g. to predators like the Common Raven [*Corvus corax*], and competitors such as *Haliaetus* spp.), and also are highly vulnerable and attractive to other Ospreys. These potential dangers may have led to an increased degree of camouflage of chicks (Osprey chicks are brown, not white, and juvenile plumage is mimetic to nest color). We suggest that it has led also to three major behavioral characteristics of Ospreys: (1) the very high intensity of guarding and attentiveness by female Ospreys; (2) the large size of the repertoire and the ritualization (in terms of conspicuousness) of displays, as visual signals need to be detected and interpreted at long distances and, thus, must be unambiguous; and (3) the existence of numerous unmistakable motivational signals (alarm, upright, and virtually all calls), which seem to be especially well developed in the Osprey. These signals are clearly visible and audible, and probably clear indicators of motivation to conspecifics and heterospecifics.

ACKNOWLEDGMENTS

Fieldwork was funded by Réserve Naturelle de Scandola (Parc Naturel Régional de la Corse). Many people helped with field work, but particular thanks are due to J.-P. Cantera, A. Delestrade, F. Finelli, I. Guyot, O. Patrimonio, and people from the Fonds d'Intervention pour les Rapaces. A. Huggins and S. J. G. Hall kindly improved the English. We acknowledge with gratitude J. C. Bednarz, J. Hagan, C. Hubert, M. Marquiss, and G. D. Schnell for their comments and advice on an earlier draft. We are indebted to L. Ruchon who drew the figures.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behaviour: Sampling methods. Behaviour 49:227–267.

ANDERSSON, S., AND C. G. WIKLUND. 1987. Sex role partitioning during offspring protection in the Rough-legged Buzzard *Buteo lapogus*. Ibis 129:103–107.

BEER, C. G. 1982. Conceptual issues in the study of communication. Pages 279–310 *in* Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.

BIRKHEAD, T. R., AND C. M. LESSEL. 1988. Copulation behaviour of the Osprey *Pandion haliaetus*. Anim. Behav. 36:1672–1682.

BRETAGNOLLE, V. 1988. Social behaviour of the Southern Giant Petrel *Macronectes giganteus*. Ostrich 59:116–125.

BRETAGNOLLE, V., J.-C. THIBAULT, AND J.-M. DOMINICI. 1994. Head patterns allow field identification of individual Ospreys. J. Wildl. Manage. In press.

BROSSET, A. 1973. Etude comparative de l'ontogénèse des comportements chez les rapaces Accipitridés et Falconidés. Z. Tierpsychol. 32:386–417.

CAIRNS, D. K. 1986. Plumage colour in pursuit-diving seabirds: Why do penguins wear tuxedos? Bird Behav. 6:58–65.

CRAMP, S., AND K. E. L. SIMMONS. (EDS.). 1980. The

birds of the western Palearctic, vol. 2. Oxford Univ. Press, Oxford.

DAWSON, J. W., AND R. W. MANNAN. 1991. Dominance hierarchies and helper contribution in Harris' Hawks. Auk 108:649–660.

DENAUROIS, R. 1987. Le Balbuzard (*Pandion haliaetus* L.) aux îles du Cap Vert. Annali del Museo di Storia Naturale di Genova 86:657–681.

EDWARDS, T. C. 1989. The ontogeny of diet selection in fledgling Ospreys. Ecology 70:881–896.

ELLIS, D. H. 1979. Development of behavior in the Golden Eagle. Wildl. Monogr. 70.

FAABORG, J., T. DE VRIES, C. B. PATTERSON, AND C. R. GRIFFIN. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galapagos Hawk (*Buteo galapagoensis*). Auk 97:581–590.

FAABORG, J., AND J. C. BEDNARZ. 1990. Galapagos and Harris' hawks: Divergent causes of sociality in two raptors. Pages 357–383 *in* Cooperative breeding in birds (P. B. Stacey and W. D. Koenig, Eds.). Cambridge Univ. Press, Cambridge.

GARGETT, V. 1990. The Black Eagle. Acorn Books, Randburgh, South Africa.

GREEN, R. 1976. Breeding behaviour of Ospreys *Pandion haliaetus* in Scotland. Ibis 118:475–490.

GREENE, E. P. 1987. Individuals in an Osprey colony discriminate between high and low quality information. Nature 329:239–241.

GREENE, E. P., AND B. FREEDMAN. 1986. Status of the Osprey in Halifax and Lunenburg counties, Nova Scotia. Can. Field-Nat. 100:470–473.

HAGAN, J. M., AND J. R. WALTERS. 1990. Foraging behavior, reproductive success, and colonial nesting in Ospreys. Auk 107:506–521.

HAILMAN, J. P. 1989. The organization of major vocalizations in the Paridae. Wilson Bull. 101:305–343.

JAMIESON, I., N. SEYMOUR, AND R. P. BANCROFT. 1982. Time and activity budgets of Ospreys nesting in northeastern Nova Scotia. Condor 81:439–441.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca.

JOUVENTIN, P. 1982. Visual and vocal signals in penguins, their evolution and adaptative characters. Advances in Ethology 24. Porey, Berlin.

KEAR, J. 1970. The adaptive radiation of parental care in waterfowl. Pages 357–391 *in* Social behaviour in birds and mammals: Essays on the social ethology of animals and man (J. H. Crook, Ed.). Academic Press, London.

KROODSMA, D. E., AND E. H. MILLER. 1982. Acoustic communication in birds. Academic Press, New York.

MCKINNEY, F. 1965. The comfort movements of Anatidae. Behaviour 25:120–220.

MILLER, E. H. 1989. Description of bird behavior for comparative purposes. Curr. Ornithol. 5:347–394.

MOCK, D. W. 1980. Communication strategies of Great Blue Herons and Great Egrets. Behaviour 72:156–170.

MØLLER, A. P. 1987. Copulation behaviour in the Goshawk, *Accipiter gentilis*. Anim. Behav. 35:755–763.

MOYNIHAN, M. 1955. Type of hostile display. Auk 72:247–259.

MUELLER, H. C. 1990. The evolution of reversed sexual dimorphism in size in monogamous species of birds. Biol. Rev. 65:553–585.

MUELLER, H. C., AND K. MEYER. 1985. The evolution of reversed sexual dimorphism in size: A comparative analysis of the Falconiformes of the western Palearctic. Curr. Ornithol. 2:65–101.

NEWTON, I. 1979. Population ecology of raptors. T. & A. D. Poyser, Calton, United Kingdom.

PALMER, R. S. (ED.). 1988. Handbook of North American birds, vol. 4. Yale Univ. Press, New Haven, Connecticut.

POOLE, A. F. 1989a. Ospreys. Cambridge Univ. Press, Cambridge.

POOLE, A. F. 1989b. Regulation in Osprey *Pandion haliaetus* populations: The role of nest site availability. Pages 227–234 *in* Raptors in the modern world (B.-U. Meyburg and R. D. Chancellor, Eds.). World Working Group on Birds of Prey, Berlin.

POSTUPALSKY, S. 1989. Osprey. Pages 297–313 *in* Lifetime reproduction in birds. Academic Press, London.

RATCLIFFE, D. 1980. The breeding cycle: Pairing and courtship. Pages 185–204 *in* The Peregrine Falcon. T. & A. D. Poyser, Calton, United Kingdom.

RICHARD, J.-P. 1991. Sound analysis and synthesis using an amiga micro-computer. Bioacoustics 3:45–60.

ROSENFIELD, R. N., AND J. BIELEFELDT. 1991. Vocalizations of Cooper's Hawk during the pre-incubation stage. Condor 93:659–665.

SAÏLLER, E. 1977. Les parades et accouplements des balbuzards pêcheurs en Corse. Nos Oiseaux 34: 65–72.

SCHLEIDT, W. M., G. YAKALIS, M. DONNELLY, AND J. MCGARRY. 1984. A proposal for a standard ethogram, exemplified by an ethogram of the Blue Breasted Quail (*Coturnix chinensis*). Z. Tierpsychol. 64:193–220.

SLATER, P. J. B. 1983. The study of communication. Pages 9–42 *in* Animal behaviour, vol. 2. (T. R. Halliday and P. J. B. Slater, Eds.). Blackwell Scientific Publications, Oxford.

SMITH, W. J. 1977. The behavior of communicating. Harvard Univ. Press, Cambridge, Massachusetts.

STANDEN, P. J. 1980. The social display of the Chilean Teal *Anas flavirostris flavirostris*. J. Zool. (Lond.) 191:293–313.

STINSON, C. H., J. LAUTHNER, AND T. R. RUSSELL. 1988. Breeding behavior of Ospreys in northwestern Washington. Murrelet 69:24–27.

THIBAULT, J.-C., AND F. BOUVET. 1983. Les caractér-

istiques du nid du balbuzards pêcheurs *Pandion haliaetus* en Corse. Nos Oiseaux 37:65–73.

THIBAULT, J.-C., AND O. PATRIMONIO. 1989. Note sur les mouvements des jeunes balbuzards pêcheurs *Pandion haliaetus* nés en Corse (Méditerrannée). Oiseau. Rev. Fr. Ornithol. 59:171–175.

THIBAULT, J.-C., AND O. PATRIMONIO. 1991. Some aspects of breeding success of the Osprey *Pandion haliaetus* in Corsica, west Mediterranean. Bird Study 38:98–102.

TINBERGEN, N. 1959. Comparative studies of behaviour of gulls (Laridae): A progress report. Behaviour 15:1–70.

TUBBS, C. R. 1974. The Buzzard. David and Charles, London.

VANTETS, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. Ornithol. Monogr. 2.

WARD, P., AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as 'information centers' for food finding. Ibis 115:517–534.

WATSON, D. 1977. The Hen Harrier. T. & A. D. Poyser, Calton, United Kingdom.

WILSON, R. P., P. G. RYAN, A. JAMES, AND M.-P. T. WILSON. 1988. Conspicuous coloration may enhance prey capture in some piscivores. Anim. Behav. 35:1558–1560.

ZAHAVI, A. 1987. The theory of signal selection and some of its implications. Pages 305–327 *in* Proceedings of the International Symposium of Biological Evolution (V.P. Delfino, Ed.). Adriatica Editrica, Bari, Italy.