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TIME AND ACTIVITY BUDGET OF OSPREYS NESTING IN NORTHERN CALIFORNIA

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Time and activity budgets provide quantitative descriptions of an animal's behavior, and aid in assessing its modes of reproduction and foraging (Orians 1961, King 1974). Hence, they have been obtained for a diverse array of birds (e.g., Verbeek 1972, Kushlan 1977, Wakeley 1978 and references therein), including several species of raptors (Stendell 1972, Balgooyen 1976, Tarboton 1978, Wakeley 1978; J. R. Koplin and co-workers, unpubl. data). Green (1976) and Stinson (1978) recently studied time and activity budgets of Ospreys (*Pandion haliaetus*) nesting in Scotland and Virginia, respectively. However, Green measured only certain activities during the breeding season, and Stinson studied Ospreys only after the eggs hatched. My objectives were to compile a detailed time and activity budget of Ospreys nesting in northern California, compare the budgets of Ospreys nesting in various locations, and document and assess the division of labor exhibited between the sexes by nesting Ospreys.

STUDY AREA AND METHODS

I observed three pairs of Ospreys nesting in northern California. Nest 1 was 1.6 km east of Humboldt Bay, Humboldt County, on the top of a 38-m redwood (*Sequoia sempervirens*) snag on a hillside vegetated primarily with the second-growth redwoods. The closest known Osprey nest was approximately 6.5 km away. Nests 2 and 3 were on the southeast and southwest sides, respectively, of a 0.8-ha marsh 0.2 km east of Eagle Lake, Lassen County. Nest 2 was in the top of an 11-m Jeffrey pine (*Pinus jeffreyi*) snag, and nest 3 was 0.8 km away on the top of a powerline pole; both were in large openings bounded by marsh or by a forest of predominantly Jeffrey pines and western junipers (*Juniperus occidentalis*). Nesting Ospreys were abundant at Eagle Lake, but most other nests were located on the west shore of the lake, a minimum of 3.2 km from nests 2 and 3.

The climate of coastal Humboldt County is moderate with dry and cool summers. Average annual precipitation, predominantly rain, is about 150 cm and falls primarily during winter. Mean daily temperatures during the 1974 breeding season ranged from 9.8° to 15.1°C. The climate at Eagle Lake is more extreme than that of coastal Humboldt County: average annual precipitation ranges from 25 to 203 cm, part of which falls as snow. Daily temperatures during the study period at Eagle Lake averaged 2°C.

I determined the sex of individual Ospreys by comparing breast-streaking and observing copulations (Macnamara 1977). Males at nests 1, 2, and 3 are referred to as male 1, male 2, and male 3, respectively; females have similar designations.

The behavior of nesting Ospreys was classified into two basic categories, flying and non-flying. Flying activities included flights to obtain nest material, courtship flights, flights involved with fishing, miscellaneous flights, and some aggressive interactions. Non-flying activities included perching on trees and nests, nest-building, mating, incubation, brooding, some aggressive interactions, feeding, and giving food to nestlings. Distinctions between most behaviors are obvious, but several activities need clarification. Nest-building included both placement of new material and rearrangement of old material in the nest. Aggressive interactions included all intraspecific interactions not involving mates and all interspecific interactions; some of the these involved flying and others consisted only of vocalizations. A nestling taking a piece of fish from the bill of an adult was termed "giving food to nestlings."

The breeding season was divided into five phases. (1) The pre-incubation phase began when Ospreys arrived in a nesting area and ended when the first egg was laid. (2) The incubation phase began when eggs were laid and ended when they hatched. (3) The nestling phase included the period during which the nestlings were present, but not yet exercising their wings. (4) The fledging phase included the period during which nestlings were exercising their wings, but not yet flying. (5) The post-fledging phase began when young took their first flights and terminated when all Ospreys left the nesting area. Average daylength was 14.0, 15.5, 15.75, 15.25, and 14.5 h during the five respective phases. Ospreys at nest 1 were observed for 397 h, spread throughout the entire 1974 breeding season (20 March to 18 September). Ospreys at nests 2 and 3 were observed for 96 and 50 h, respectively, during the pre-incubation phase of the 1975 breeding season (8 April to 3 May). Observation periods usually lasted from dawn until dusk (36 days), although some periods were of shorter duration (9 days).

The chronological time at the beginning of each activity and elapsed time of each activity were recorded. Analyses were stratified by sex and by phase of breeding season. Because unequal hours of observation were conducted during different phases, data were made comparable by calculating the frequency of occurrence per hour of observation and percent of observation time an activity occurred; all results refer to daylight time only.

RESULTS

Females rarely flew during the pre-incubation phase, while males flew for about one-fifth of the time (Table 1). Female 1 rarely flew during the first four phases, but she increased flying activities substantially during the post-fledging phase, primarily by increasing time spent fishing. Percent flying time of male 1 during the pre-incubation, incubation, and fledging phases was less than flying time during the nestling and fledging phases, primarily because time spent fishing increased during the latter two phases.

TABLE 1. Percent of daylight time Ospreys engaged in various activities at nest 1 during the 1974 breeding season and at nests 2 and 3 during the pre-incubation phase of the 1975 breeding season.[a]

	Nest 1										Nest 2		Nest 3	
	Pre-incubation		Incubation		Nestling		Fledging		Post-fledging		Pre-incubation		Pre-incubation	
Activity	F	M	F	M	F	M	F	M	F	M	F	M	F	M
Obtaining nest material	0.6	2.8	0.1	1.6	1.1	0.4	1.1	0	0.1	0.3	0.9	0.4	0.6	4.1
Courtship flight	0.4	1.8	0.1	0.1	0	0	0	0	0	0	1.2	1.9	1.3	1.2
Fishing	0	13.7	0	16.4	0	25.7	1.2	20.2	26.1	26.4	0.7	7.9	0	8.6
Miscellaneous flight	1.1	2.2	0.6	3.9	0.5	1.3	1.6	1.4	1.6	1.7	2.6	7.0	3.0	6.5
Aggressive flying interactions	0.3	1.0	0.3	1.0	0.2	0.2	0.2	0.2	0.2	1.0	1.0	1.8	0.2	0.6
SUBTOTAL (flying)	2.4	21.5	1.1	23.0	1.8	27.6	4.1	21.8	28.0	29.4	6.4	19.0	5.1	21.0
Perch on trees	11.7	38.6	2.0	32.1	3.4	45.6	21.4	71.4	48.0	65.6	40.2	47.0	53.5	35.7
Perch on nest	75.8	30.1	16.8	11.6	49.4	16.5	60.9	1.5	16.5	1.6	43.6	11.9	30.9	17.7
Nest-building	0.3	1.1	0.3	0.3	0.4	0.2	0.2	TR	TR	TR	0.3	0.3	0.5	1.0
Mounting	0.3	0.3	TR	TR	0	0	0	0	0	0	0.1	0.1	0.2	0.2
Copulation	0.1	0.1	TR	TR	0	0	0	0	0	0	TR	TR	0.1	0.1
Incubation	0	0	70.3	25.7	0	0	0	0	0	0	0	0	0	0
Brooding	0	0	0	0	31.7	1.2	0	0	0	0	0	0	0	0
Aggressive non-flying interactions	0.4	TR	0.5	0.2	0.2	0.1	TR	0	TR	TR	0.1	0.5	TR	0.7
Feeding	7.6	7.2	4.3	3.9	2.1	6.4	2.3	3.9	1.0	2.9	5.3	8.5	5.8	9.7
Giving nestlings food	0	0	0	0	10.5	0.1	9.6	0.6	3.0	0	0	0	0	0
SUBTOTAL (non-flying)	96.2	77.4	94.2	73.8	97.7	70.1	94.4	77.4	68.5	70.1	89.6	68.3	91.0	65.1
Unknown	1.6	1.2	4.6	3.2	0.6	2.1	1.7	0.9	3.5	0.5	4.0	12.7	4.0	14.2

[a] Number of hours of observation at nest 1 = 38 (pre-incubation), 101 (incubation), 143 (nestling), 45 (fledging), and 70 (post-fledging). Number of hours at nest 2 = 96; at nest 3 = 50. Abbreviations in table are: F = female; M = male; TR = activity occurred for less than 0.05% of daylight time.

TABLE 2. Rate of fish and nest material deliveries by Ospreys at nest 1 during the 1974 breeding season and at nests 2 and 3 during the pre-incubation phase of the 1975 breeding season. Number of hours of observation are the same as in Table 1.

Nest and phase	No. fish delivered per hour			No. nest material items delivered per hour		
	Female	Male	Combined	Female	Male	Combined
Nest 1						
Pre-incubation	0	0.26	0.26	0.08	0.39	0.47
Incubation	0	0.22	0.22	0.02	0.09	0.11
Nestling	0	0.42	0.42	0.33	0.04	0.37
Fledging	0.02	0.47	0.49	0.48	0	0.48
Post-fledging	0.23	0.44	0.67	0.05	0.01	0.06
Nest 2						
Pre-incubation	0.02	0.18	0.20	0.15	0.14	0.29
Nest 3						
Pre-incubation	0	0.20	0.20	0.16	0.61	0.77

Females generally were sedentary most of the day (Table 1). During the post-fledging phase, however, female 1 spent more time in flying activities. Males performed non-flying activities for two-thirds to three-fourths of the time during the pre-incubation phase, and male 1 did not fly for approximately three-fourths of the time during the entire season (Table 1).

Flights to obtain nest material occurred throughout the season, but never occupied more than 4.1% of daylight time (Table 1). Males delivered most of the nest material prior to the date eggs were laid; after the eggs hatched in nest 1, female 1 brought most of the material to the nest (Table 2). The combined rates of deliveries during the incubation phase and during the post-fledging phase were much lower than during the other three phases. Nest-building also occupied only a small fraction of daylight time (Table 1).

The frequency of mating at all three nests gradually increased throughout the pre-incubation phase, reached a peak two to six days prior to initiation of egg-laying, and then decreased. An average of 46.5% of mating attempts were completed; differences among the three pairs were not significant ($\chi^2 = 0.191$, 2 d.f., $P > 0.90$). Courtship flight and mating attempts occupied less than 2.5% of the time during the pre-incubation phase and less than 1% during the incubation phase; they were not seen thereafter (Table 1).

Eggs at nest 1 were incubated for 96.1% of daylight time. Female 1 performed 73.2% of the incubation; male 1 generally incubated the eggs while the female was feeding. The percent of time each sex incubated eggs did not fluctuate greatly from one observation period to the next (Fig. 1). After the eggs hatched, female 1 performed 96.3% of all brooding. She brooded the two nestlings for most of the day during their first two weeks, but subsequently brooded much less often (Fig. 1). Male 1 brooded nestlings for 11.4% of the first day after eggs began hatching, but subsequently brooded them only rarely.

Female 2 was observed fishing twice during the pre-incubation phase, both times near its beginning; she was the only female I saw fishing during this phase. Female 1 rarely fished during the first four phases, but did so often during the post-fledging phase (Table 1). Males spent more time fishing than females, except during the post-fledging phase at nest 1 (Table 1).

Fish deliveries to nesting areas (Table 2) paralleled the pattern of fishing. Males delivered all of the fish at nest 3 and 89.5% of the fish at nest 2 during the pre-incubation phase. Male 1 delivered all of the fish at nest 1 during the first three phases, 95.9% during the fledging phase, and 70.5% during the post-fledging phase. He delivered fish during the post-fledging phase at approximately the same rate as during the previous two phases (Table 2); during the nestling and fledging phases he transferred fish to the female, but during the post-fledging phase most fish were transferred directly to the young. The total delivery rate at nest 1 was highest during the post-fledging phase, when female 1 delivered 29.5% of the fish. During this phase, I observed her feeding on 16 fish, 12 of which she brought to the nesting area and four of which the male brought.

Female 1 gave food to nestlings 125 times and male 1 gave them food four times dur-

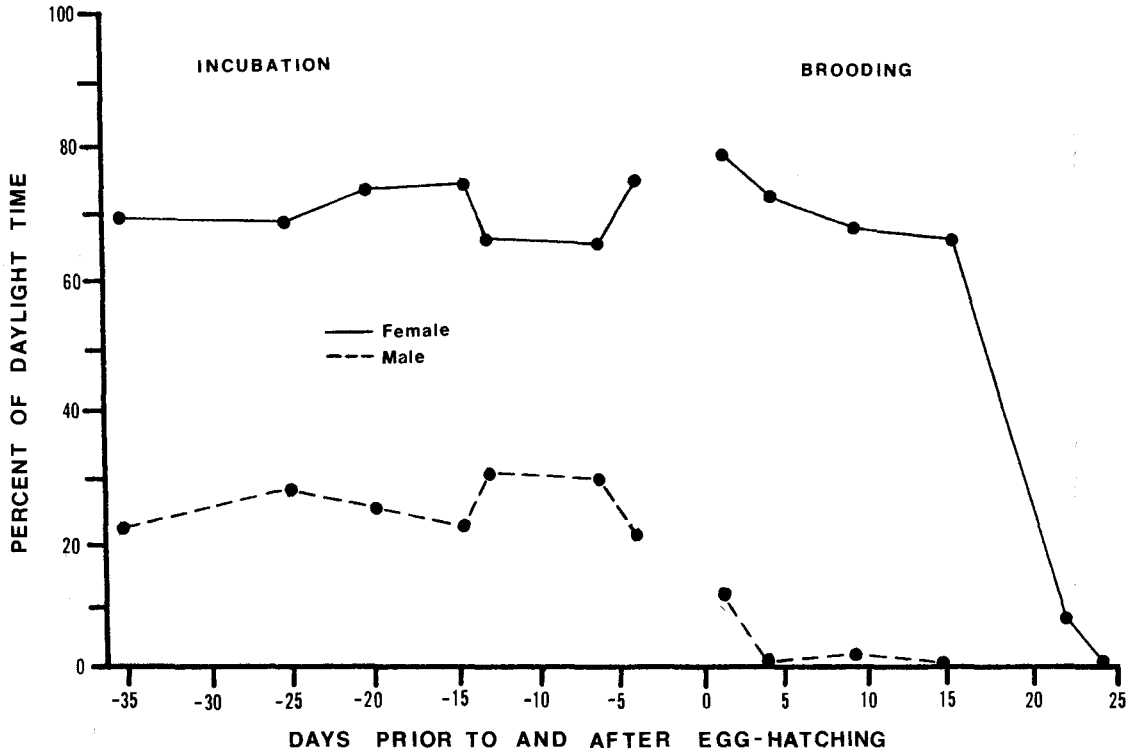

FIGURE 1. Percentages of daylight time female and male Ospreys engaged in incubation and brooding in relation to number of days prior to and after first egg hatched at nest 1 (Humboldt County, California) during the 1974 breeding season. Day 0 indicates the day of hatching.

ing the nestling and fledging phases; she spent much more time than the male feeding nestlings (Table 1). During the post-fledging phase, only the female gave food directly to the nestlings, but both adults usually provided food to young by leaving an entire or partially consumed fish in the nest; the young then fed themselves the fish.

Aggressive interactions with other Ospreys during the pre-incubation phase were more frequent at nests 2 and 3 than at nest 1, but these conflicts occupied little time (Table 1). Aggressive interactions of the Ospreys with other species were even less frequent and never occupied more than 1% of the time.

DISCUSSION

In the following comparison of the nesting behavior of Ospreys in different localities, references to Scotland are from Green (1976) and those to Virginia are from Stinson (1978).

During the breeding season Ospreys, especially females, are relatively inactive until the young fledge. Females in Virginia and California spend more than 90% of the day at or near the nest (i.e., not flying) before the young fledge; during the post-fledging phase, though, females in both places are much more active. Males always are more active than females, but after the eggs hatch still spend one-third to three-fourths of the day at or near the nest. Differences between localities (see Table 1 of this study and Tables 1 and 5 in Stinson) could result from: variation in individual behavior; the possibility that Ospreys in Virginia also may have perched when away from the nest site; seasonal differences in prey availability; and effects of weather on hunting success (Grubb 1977) and subsequent amount of time required for hunting.

Seasonal differences in obtaining nest material exist between the sexes. In Scotland and California, males deliver most nest material prior to egg-laying, whereas females deliver most nest material after eggs hatch. Females in Virginia bring slightly more nesting material than males during the nestling phase. In general, Ospreys deliver most nest material during the pre-incubation, nestling, and fledging phases, which enables them to repair and maintain nests without disturbing eggs during incubation.

Species with long migrations and extended breeding seasons must begin nest-building and egg-laying quickly, so that the young have sufficient time to complete their

development (Matray 1974); little time can be spent on pair formation or territorial disputes (Ames 1964). Ospreys in California spend little time courting and begin nest-building shortly after arrival in nesting areas. The pattern of an increasing number of mating attempts prior to egg-laying could aid in synchronization of the hormonal systems of the two sexes (Beer 1973, Follett 1973). With the male and female returning to the nest site of the previous year within a few days of each other (Allen 1892, Ames 1964, Green 1976), mated Ospreys could eliminate the time required to find a new nest site and reduce the need for extensive courtship (see Emlen and Oring [1977] for a thorough discussion of the advantages of long-term monogamy). Minimizing the time spent in courtship might be particularly critical in areas with climatic extremes; the pre-incubation phase at Eagle Lake was approximately 13 days shorter than in climatically moderate coastal Humboldt County. In Scotland, egg-laying starts an average of 12 days after both birds arrive at the nest site; climatic conditions were not described, but the short pre-incubation period probably is both necessary and allowed by quick and efficient courtship.

Females in Scotland and California perform most incubation, but males frequently take over incubation after delivering fish to females; in California, males incubated eggs for 25% or more of the day (Garber and Koplin 1972, this study). Females perform virtually all brooding; as young grow older, however, total time spent brooding by females decreases. In all three localities (see also Stinson 1977), males usually deliver fish directly to females, who then present pieces of fish to the nestlings.

Patterns of fishing and fish deliveries prior to the post-fledging phase are very similar; males in all three localities deliver almost all fish eaten by females and young. After the young fledge, however, the relative roles of the sexes in fishing vary greatly among localities. Females deliver 60.4% of the fish in Virginia, 29.5% in California, and less than 5% in Scotland during the post-fledging phase.

Patterns of fish deliveries also vary for the post-fledging phase. Females and males in Virginia deliver the same number of fish per hour after young fledge as males delivered before young fledged, but weights of the fish delivered increase throughout the nestling phase and presumably throughout the post-fledging phase. At nest 1 in California, however, Ospreys delivered increasing numbers of equal-sized fish as the season progressed (unpubl. data). Females and males in Virginia and California thus deliver a greater total weight of fish per hour after the young fledge than do males before young fledge. In Scotland, the total weight of fish delivered per hour is the same before and after fledging, with a slight decline around fledging. Since females in Scotland rarely deliver fish to nests during the post-fledging phase, they may capture and consume fish without returning to the nest during that phase. If this is true, then the total weight of fish consumed per day by adults and their young actually would increase as the season progresses, but the increase would not be apparent to observers.

Ospreys exhibit a distinct division of labor between sexes in caring for the young and obtaining food. One factor responsible for this habit may be the altricial growth of the nestlings. Altricial young are poikilothermic for several days after hatching and must be brooded by an adult until they are able to thermoregulate (Ricklefs 1974); they also require some protection even after being able to thermoregulate. Therefore, in monogamous birds with altricial young, both adults usually must help raise the young to independence. By dividing tasks, a female Osprey is free to brood the young, while the male forages for food for the entire family.

Another factor related to the division of labor may be the high nutrient quality and energy content of fish. Although capture of such prey may require considerable expenditure of energy, energy intake is sufficiently high that only one member of a breeding pair needs to forage (at least until young fledge) in order to fulfill the energy requirements of the pair and their offspring.

Females brood young extensively only during the first few weeks of the nestling phase; subsequently, they perch near the nest for much of the day. After young fledge, females spend much less time both on the nest and in the nesting area (Stinson 1978, this study). In comparison with males, females remain relatively inactive prior to fledging of the young. Two possible reasons for this difference are: (1) Foraging by males might be less expensive energetically than foraging by females, because of the relationship between body size and metabolism (Mosher and Matray 1974). This would make more energy available to the pair and their offspring. (2) The energy requirement for egg-laying by female raptors, while relatively lower than that of most other birds,

still necessitates additional energy intake (Ricklefs 1974). Therefore, females could conserve energy by remaining relatively sedentary (e.g., Applegate 1977).

When the young approach the time of fledging, they no longer need to be protected from ambient conditions, and their energetic requirements may exceed the resources that the male is capable of providing. Therefore, during the time after the young have fledged, both adults forage; females procure some of their own food and often provide food to the young.

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