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## **Role of Helpers in the Sentinel Behaviour of the Florida Scrub Jay (*Aphelocoma c. coerulescens*)**

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### **Abstract**

Two independently conceived and executed field studies using somewhat different methodologies tested the hypothesis that non-breeding helpers of the Florida scrub jay (*Aphelocoma c. coerulescens*) contribute importantly to antipredator sentinel behaviour. Specifically, we made four predictions: 1. Helpers participate to a non-trivial degree in sentinel behaviour; 2. Breeding pairs with helpers spend less time on sentinel behaviour and hence more time foraging; 3. Breeders with helpers have more protected foraging time; and 4. Groups with helpers have greater total sentinel time.

Results of the two studies agreed on most major points and even, in many cases, on minor points and quantitative aspects. Non-breeding adult helper birds participated in sentinel watches almost as much as breeders in their group. In winter, breeding pairs with one or more helpers decreased their own sentinel time compared with that of unassisted pairs. However, in the one study, the concomitantly increased available foraging time of breeders was no better protected by another group member being on sentinel than in the lone pairs. Results of the other study showed a significant increase of protected foraging time for breeding males only. In winter, groups with helpers did not have increased total sentinel time; time was either the same (Study A) or significantly less (Study B). During nesting, breeders with helpers did not decrease their sentinel effort relative to lone pairs. Instead, groups with helpers had a sentinel for more time. These results are interpreted as indicating that, in winter, sentinel behaviour is more important to antiraptor defense in lone pairs than larger groups. In groups with helpers the mere addition of extra pairs of eyes and ears may render formal sentinel behaviour less necessary, so breeders can decrease their sentinel time and increase their foraging time. During nesting, additional sentinels may be important for increased nest protection. The presence of helpers contributing to predator detection may thus be an important factor in the better annual survival and nesting success of breeders that have helpers (WOOLFENDEN & FITZPATRICK 1984).

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## Introduction

Numerous animals show vigilance behaviour (PULLIAM 1973; GOODWIN 1976; BERTRAM 1980; WARD 1985; WICKLER 1985; ELGAR 1989), and studies of some social species have reported group coordination of vigilance (CORTI & MELCHER 1944; JENKINS 1944; ANDREWS & NAIK 1970; BALDA et al. 1972; FORSHAW 1973; GASTON 1977; RASA 1977, 1983, 1986; VERBEEK & BUTLER 1981; MORAN 1984; WICKLER 1985; HORROCKS & HUNTE 1986; FERGUSON 1987). MCGOWAN & WOOLFENDEN (1989) showed that sentinel coordination exists in the cooperatively breeding Florida scrub jay (*Aphelocoma c. coerulescens*) in which one jay perches watchfully at a vantage point while the other members of the group forage nearby. The principal aims of the present study were to quantify the degree of participation in sentinel behaviour by non-breeding, adult 'helper' individuals and to evaluate the effect of their participation on the sentinel behaviour and foraging of the breeding pair in the group to which they belong.

The Florida scrub jay is a non-migratory, permanently paired, permanently territorial resident of the oak scrub habitat of the Florida peninsula. The jay's life history, territoriality, social organization and demography have been studied extensively (WOOLFENDEN & FITZPATRICK 1984, 1990). Each territory is defended by a breeding pair; the pair may live with one or more juvenile offspring of the previous nesting season (i.e. less than 1-yr old) and one or more older, non-breeding helpers (age 1 yr or older). Helpers are frequently offspring of earlier breeding seasons, but their relationship to the breeding pair varies greatly, and a few adopted helpers have only distant kinship to the breeders (WOOLFENDEN & FITZPATRICK 1984). Breeders with no helpers have a higher annual mortality than breeders with at least one helper (WOOLFENDEN & FITZPATRICK 1984), and also have lower nesting success. The immediate cause of death in adult scrub jays is difficult to determine, but strong circumstantial evidence suggests that predation is the overwhelming factor (WOOLFENDEN & FITZPATRICK 1984). Similarly, nest failures are caused primarily by predation rather than factors such as failure of eggs to hatch or starvation of nestlings (WOOLFENDEN & FITZPATRICK 1984). Table 1 provides a taxonomic list of potential jay predators known from the jays' habitat in the study area (compare with list of predators known to be mobbed by jays; FRANCIS et al. 1989). The table also provides a first estimate of the relative abundance of different predatory species likely to be encountered by the jays.

MCGOWAN & WOOLFENDEN (1989) showed that sentinel behaviour is a coordinated group activity. The time during which two or more birds act as sentinels simultaneously proved to be a small fraction of that expected on a random basis of no coordination among individuals, and exchanges of sentinels were more frequent than expected by chance. Sentinel behaviour is well suited to detecting dangerous aerial predators. The Cooper's hawk, sharp-shinned hawk, northern harrier and merlin (Table 1 for Latin names) all take prey by surprise by flying rapidly and close to the top of the scrub, which averages about 2 m in height. The great horned owl, when hunting near dawn or dusk, behaves similarly. Accipiters may also drop from great heights onto prey (K. J. MCGOWAN pers. obs.). A jay

**Table 1:** Potential jay predators recorded in the habitat of the Florida scrub jay during 1488 h of field work by MCGOWAN between 11 Jan. 1982 and 5 Aug. 1987 (taxonomically related predators grouped together)

Predator species	Encounters	Status <sup>1</sup>
Osprey ( <i>Pandion haliaetus</i> )	30	
American swallow-tailed kite ( <i>Elanoides forficatus</i> )	21	
Bald eagle ( <i>Haliaeetus leucocephalus</i> )	14	
Northern harrier ( <i>Circus cyaneus</i> )	87	DF
Sharp-shinned hawk ( <i>Accipiter striatus</i> )	41	DF
Cooper's hawk ( <i>Accipiter cooperii</i> )	46	DF
<i>Accipiter</i> sp.	7	DF
Red-shouldered hawk ( <i>Buteo lineatus</i> )	10	
Broad-winged hawk ( <i>Buteo platypterus</i> )	3	
Short-tailed hawk ( <i>Buteo brachyurus</i> )	1	
Red-tailed hawk ( <i>Buteo jamaicensis</i> )	130	DF
Crested caracara ( <i>Polyborus plancus</i> )	1	
American kestrel ( <i>Falco sparverius</i> )	39	
Merlin ( <i>Falco columbarius</i> )	15	DF
Barn owl ( <i>Tyto alba</i> )	1	
Eastern screech-owl ( <i>Otus asio</i> )	3	DF
Great horned owl ( <i>Bubo virginianus</i> )	78	DF
Burrowing owl ( <i>Athene cunicularia</i> )	1	
Gray fox ( <i>Urocyon cinereoargenteus</i> )	1	
Bobcat ( <i>Lynx rufus</i> )	7	DF
Raccoon ( <i>Procyon lotor</i> )	0 <sup>2</sup>	
Alligator ( <i>Alligator mississippiensis</i> )	1	
Corn snake ( <i>Elaphe guttata</i> )	1	
Pine snake ( <i>Pituophis melanoleucus</i> )	3	
Indigo snake ( <i>Drymarchon coras</i> )	9	DF
Black racer ( <i>Coluber constrictor</i> )	11	uf
Eastern coachwhip ( <i>Masticophis flagellum</i> )	10	DF
Eastern coral snake ( <i>Micrurus fulvius</i> )	3	

<sup>1</sup> DF = documented predator, predation on adults or nests probably frequent; uf = undocumented predator, predation possibly frequent

<sup>2</sup> Footprints daily, nest predation probably frequent

on sentinel duty perches at the top of the scrub on an exposed perch and does virtually nothing but look around in all directions of its hemispheric view, especially at eye level just over the top of the scrub. When sighting one of the aforementioned raptors at a distance, the sentinel gives one of several calls that alert other group members (ELOWSON & HAILMAN 1991), which may fly to a

perch and look in the direction the sentinel is looking. If the sentinel first detects the raptor at close range, it gives a different call and dives into the scrub; this alarm call causes other birds to flee immediately to cover, as shown through playback experiments. In some cases the sentinel may call and stay perched while others hide.

To summarize, certain raptors pose great danger to Florida scrub jays. The jays' sentinel behaviour effectively detects these raptors, helpers participating in sentinel behaviour to some degree, and breeding adults with at least one helper survive better and have higher nesting success than those without helpers. This combination of facts suggests that an important factor in the better survival of breeders with helpers might be the role played by helpers in sentinel behaviour. This study quantifies helper participation in sentinel duty, and compares the sentinel and foraging times of breeding pairs with and without helpers in order to test the following hypotheses: 1. Helpers participate to a non-trivial degree in sentinel behaviour; 2. Breeding pairs with helpers spend less time on sentinel behaviour and more time foraging; 3. Breeders with helpers have more protected foraging time; and 4. Groups with helpers engage in greater total sentinel time. The data supported the first hypothesis but the other tests depended on time of year and, in many cases, sex of breeder.

## Methods

This report concerns two independently conceived studies on closely related aspects of the same set of problems. The methods used in the two studies were somewhat different and so are outlined separately below.

### Study Area

Both studies were carried out at Archbold Biological Station, Highlands County, south-central Florida, where the Florida scrub jay has been under intense study by WOOLFENDEN and colleagues since 1969 (WOOLFENDEN & FITZPATRICK 1990). The birds are restricted to oak-scrub habitats on ancient sand dunes. For a detailed description of the vegetation of the Station, see ABRAHAMSON *et al.* (1984). Both studies were carried out on the maintained study population of jays; every individual is colour-banded before fledging or soon after immigrating (if arriving from outside the study tract). A monthly census of the entire population is taken and territorial boundaries are mapped each spring (changing little through the year unless a male breeder dies). For details of the habitat, banding, territories, censuses, *etc.*, see WOOLFENDEN & FITZPATRICK (1984, 1990).

### Study A

One study was part of a larger research project on social development in young Florida scrub jays (MCGOWAN 1987) which included the roles of helpers in mobbing of predators, territorial defense and feeding of fledglings, as well as in sentinel behaviour. The present report documents the role of helpers in the sentinel system and their effect on behaviour of the breeding pair.

MCGOWAN followed selected groups for variable periods, recording all performance of sentinel activity by all group members within an observation period. Jays were observed in two time blocks each morning, and generally one in late afternoon. Observation periods ranged from 1 to 3 h ( $\bar{x}$  = 1.9 h). Selected groups were followed on alternate days and rotated sequentially through the three time blocks. Data were collected daily from May to Aug., 1983, and Apr. to Aug. 1984. From Sep. to Mar., 1983–84, 1984–85, and 1985–86, data were also collected on one or two weekends each

month. Observation periods were discarded if the jays were lost from view within 1 h, or if the observer's presence appeared to be affecting the jays' behaviour.

For purposes of this study, jays were divided into eight status classes (STALLCUP & WOOLFENDEN 1978): male breeders, female breeders, older male helpers (2 yr or older), older female helpers, yearling male helpers, yearling female helpers, juveniles (ages 3 mo–1 yr), and fledglings (fledged birds under 3 mo of age). Sample sizes differed among classes. Essentially all groups had a male and female breeder but none had helpers of all types. Although virtually all yearling jays act as helpers, relatively few are still helpers in subsequent years, most having died or found breeding spaces. Consequently, few older helpers of each sex were available to be observed during this study. When appropriate, data from some of the various helper classes were combined to achieve sample sizes suitable for statistical analyses.

The operational definition of sentinel behaviour for the purposes of this study was as follows: it was assumed that foraging required looking at the ground nearby so that one criterion for sentinel behaviour was looking at the ground for less than approximately 50 % of the time. Other criteria were looking in each of all four compass directions at least once approximately every 20 s, and remaining perched for at least 30 s.

Sentinel behaviour was recorded in 394 observation periods, totaling 795 h. Approximately 75 jays in about 20 groups were studied (minor variation resulted from altered group composition over time and the fact that many fledglings died before performing any or much sentinel behaviour). The amount of sentinel behaviour for each jay was calculated as the percentage of time the group was under observation and also as a percentage of the total time that a group had a sentinel. To normalize sentinel data for statistical analysis, all percentages were transformed using the arcsine function (ZAR 1980). Single-factor analysis of variance (ANOVA) was performed on the transformed data to detect differences in contributions by different group member categories (ZAR 1980) and Duncan's new multiple-range test (DNMRT) was used to find where the differences lay (STEEL & TORRIE 1980). When the underlying assumption of homogeneity of variance was not met, the Kruskal-Wallis single-factor analysis of variance by ranks (ZAR 1980) on non-transformed data was used to detect differences, and DUNN's (1964) non-parametric multiple-range test was used to find where they lay.

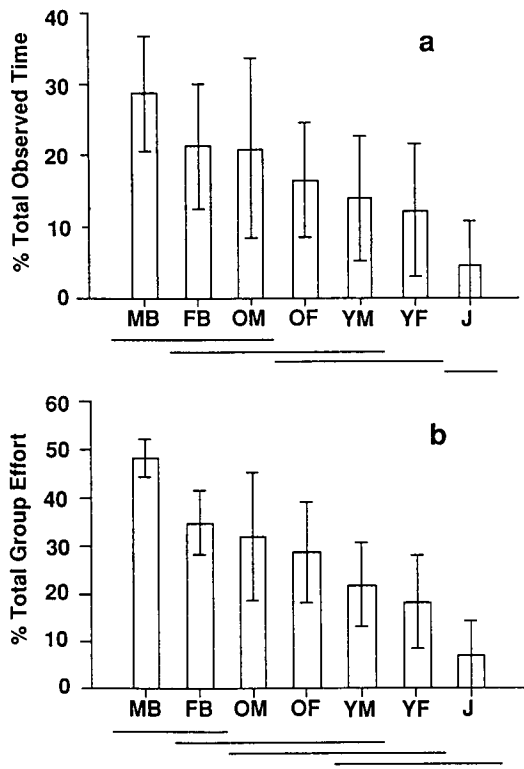
## Study B

The second study was designed by HAILMAN as an Earthwatch project, and was led by him with the aid of MCGOWAN and A. M. ELWSON. The design differed from Study A in that one group was followed for an entire day, alternating days between pairs with and without helpers. The field period was 8–24 Jan. 1985, when wintering raptors are common in jay habitat and sentinel behaviour is easily studied (MCGOWAN 1987; MCGOWAN & WOOLFENDEN 1989; present Study A). An attempt to study each group for one full day from dawn to dusk was made by using rotating teams of observers for 2.5-h watches. Teams were composed differently every day on a systematic schedule to even out any biases caused by observer combinations. Sample data comparisons were also made among teams studying the same jay group and no differences could be found.

Scrub jay individuals within a group almost always stay within sight of one another during winter days, but on the rare occasions that an individual strayed from the group it was followed by one team member. A group was sometimes lost for some portion of a watch, usually because of territorial intruders at a distant border. For various reasons some groups could not be studied and other studies had to be abandoned. A total of 10 groups was studied completely for a full day each: five breeding pairs without helpers, three groups with one helper each, one group with two helpers, and one with four.

The inability of watch teams to keep the birds under observation was a problem in two cases; the few data for groups WCPR and IBRN preclude some statistical comparisons. The mean and median proportion of 'group lost' time for groups without helpers was 0.422 and 0.440, respectively, and the values for groups with helpers were nearly identical, (0.424 and 0.450, respectively). The two distributions did not differ (Mann-Whitney U-test,  $n_1 = n_2 = 5$ ,  $U = 12$ ,  $p = 1.0$ ). Therefore, possible bias because of the inability to locate birds was unlikely to play a role in any differences found between groups with and without helpers.

For purposes of this study, a bird was defined as being on sentinel duty as soon as it assumed position on an exposed perch and began looking around in the horizontal plane. If a bird looked down frequently, as if foraging, moved from its perch to forage or fly toward intruders, or interrupted its



*Fig. 1:* Two measures of yearly sentinel performance by class in study A (M-male, F-female, B-breeder, O-older helper, Y-yearling helper, J-juvenile). Bars: means of monthly mean values, with vertical lines being one SD. Means connected by horizontal lines did not differ significantly (for statistical tests, see text)

watch in any other way than by brief maintenance activities, the activity was considered to have ended. These criteria differ slightly from those of Study A (above) and of MCGOWAN & WOOLFENDEN (1989).

Basic data were taken on preprinted forms, which included time notations made when a jay began or ended sentinel behaviour. The total duration (min) of sentinel time for each bird was calculated, and data were also broken down into portions in which the bird was on sentinel duty alone and on sentinel duty at the same time as another bird. Also calculated was the amount of time that each breeding bird was not on sentinel duty, and the proportion of that time that at least one other group member was on sentinel duty.

## Results — Study A

### Hypothesis 1: Helpers Participate Non-trivially in Sentinel Behaviour

All group members participated in sentinel behaviour to some degree, but total contributions over a year varied with status (Fig. 1). Time spent on sentinel duty throughout the year (Fig. 1a), as measured by a mean of monthly mean values, differed significantly by age/sex status (ANOVA:  $F_{6,76} = 11.07$ ,  $p < 0.001$ ;

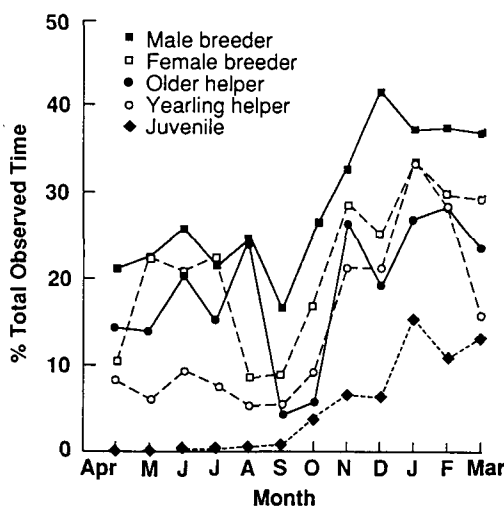


Fig. 2: Sentinel performance by class through the year (study A), as measured by percentage of total observed time (cf. Fig. 3)

DNMRT:  $p = 0.05$ ). In terms of proportion of the group's sentinel watch (Fig. 1b), status also played a significant role (Kruskal-Wallis ANOVA:  $H_6 = 53.23$ ,  $p < 0.001$ ; Dunn's test:  $p = 0.05$ ). The figure shows that whereas male and female breeders do not differ significantly in sentinel participation, the male breeder does spend more time on sentinel duty than classes of young birds (except older male helpers in Fig. 1a).

MCGOWAN & WOOLFENDEN (1989: Fig. 2a) showed that sentinel behaviour varies throughout the year, with a winter peak from Nov. to Mar., and a secondary summer peak in Jun. and Jul. Therefore, the contribution of group members by age/sex status was further assessed according to time of year. Fig. 2 plots sentinel behaviour as a percentage of total observation time by month, where it can be seen that breeders and older helpers follow the overall yearly pattern reported by MCGOWAN & WOOLFENDEN (1989). Yearling helpers show only a rudiment of the secondary summer peak in sentinel duty, and of course the dependent fledglings show none.

When sentinel contribution was expressed as a percentage of total group effort, seasonal patterns were a little different. Male breeders contributed about half the sentinel behaviour of the group throughout the year (Fig. 3), dropping a little in May–Jul., when adults are actively feeding fledglings (MCGOWAN & WOOLFENDEN 1990) and also moulting (BANCROFT & WOOLFENDEN 1982). Female breeders conformed to the overall pattern of two seasonal peaks, as did older helpers except that their summer peak is later and more restricted in time; this latter pattern may be influenced by non-breeder dispersal times, which are at their maximum in spring and early fall (WOOLFENDEN & FITZPATRICK 1984).

Analyses of variance confirmed our impression of seasonal differences in

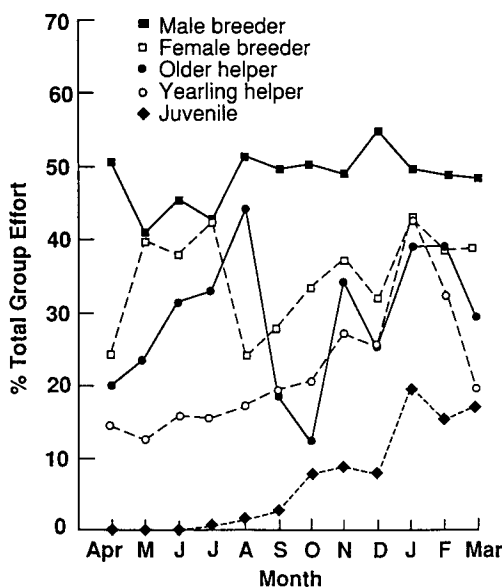


Fig. 3: Sentinel performance by class through the year (study A), as measured by percentage contribution to the group total sentinel behaviour (cf. Fig. 2)

contributions by jays of different status. Data were divided into four periods: a. late May–Jul., when families have dependent fledglings; b. Aug.–Sep., shortly after juvenile independence and during acorn harvesting (DEGANGE *et al.* 1989); c. Oct.–Mar., when sentinel occurrence was highest; and d. Apr.–early May, when families have active nests. During the period with dependent fledglings, the times spent on sentinel behaviour varied by status ( $F_{5,45} = 10.41$ ,  $p < 0.001$ ), with older adults spending the most time on sentinel behaviour and yearlings the least. Male breeders spent significantly more time on sentinel behaviour than older helpers (sexes combined), and female breeders were intermediate and not statistically separable from either. Relative contributions to total sentinel time showed similar patterns ( $F_{5,45} = 17.10$ ,  $p < 0.001$ ).

During the summer period, differences in total time also occurred ( $F_{6,37} = 19.16$ ,  $p < 0.001$ ), with the male breeders spending significantly more time on sentinel duty than females or helpers of either sex or age; juveniles and yearling female helpers spent significantly less time than female breeders or male helpers. Relative contributions to total sentinel time of the group showed the same pattern ( $F_{6,37} = 19.66$ ,  $p < 0.001$ ).

The fall–winter period is a peak time for sentinel duty, and it is also when raptor populations are highest (MCGOWAN & WOOLFENDEN 1989). Here again, the amount of sentinel behaviour varied among classes ( $F_{7,46} = 15.82$ ,  $p < 0.001$ ). Male breeders participated most and were significantly different from all other members of the group. No significant differences existed among the other members



of the group except that juveniles participated least. The results on relative contributions to total sentinel behaviour were similar ( $F_{7,46} = 21.88$ ,  $p < 0.001$ ).

Finally, during nesting, sentinel time again varied by status ( $F_{5,22} = 8.38$ ,  $p < 0.001$ ), with the male breeder spending significantly more time than any class except older female helpers. Relative contributions to total sentinel behaviour of the group were similar ( $F_{5,22} = 11.20$ ,  $p < 0.001$ ), with the male breeder making a significantly larger contribution than all but the female breeder. Note that female nest attendance (incubation and brooding) was not considered to be sentinel behaviour, even though she was vigilant at that time. Female helpers tended to spend more time on sentinel duty than did male helpers of the same age — significantly so for older helpers when considering total time, and for yearlings for group sentinel.

### **Hypotheses 2 and 3: Helpers Decrease Sentinel Time and Increase Guarded Foraging Time of Breeders**

The participation of helpers in sentinel behaviour could release breeders from some part of their own sentinel investment. During the fall-winter period, male breeders in groups with helpers participated in significantly less sentinel duty than did males of unassisted pairs (Table 2). During this period, and also during late summer, a significant negative correlation exists between the male breeder's sentinel time and the group size. Thus, during the critical fall-winter period when raptors are abundant, the male breeder with helpers has more time available for foraging and caching, because of his decreased sentinel participation. While not on sentinel duty male breeders with helpers were guarded by another sentinel for a greater percentage of the observed time than were males without helpers ( $36.4 \pm 7.1$  vs.  $24.4 \pm 10.3$ ;  $t_{13}$  on transformed data = 2.49,  $p < 0.05$ ).

For female breeders, only during the late summer period did a significant difference exist in sentinel time between those with and those without helpers (Table 2). Also only in this period, a significant negative correlation existed between the female breeder's sentinel time and group size. In winter, female breeders with helpers did not differ significantly from those without help in time spent as sentinels (Table 2), nor in protected foraging time ( $44.8\% \pm 9.4$  with help,  $41.2 \pm 6.7$  without;  $t_{13}$  on transformed data = 0.60,  $p > 0.50$ ).

The results therefore confirm the predicted decrease in sentinel behaviour of breeders having helper(s), but not at all times of the year.

### **Hypothesis 4: Groups with Helpers Display Greater Total Sentinel Time**

If helpers are making a substantial contribution to sentinel duty, then groups with helpers may display greater total sentinel time than lone pairs. This prediction was supported during the nesting period (Table 2), but at no other time. Similarly, sentinel coverage showed a significant positive correlation with group size during nesting, but at no other time of the year.

Table 2: Sentinel behavior in groups with and without helpers (study A)

Season <sup>1</sup>	Mean % sentinel time $\pm$ SD (n)		Difference		n	% sentinel/group r <sub>s</sub>
	No helpers	$\geq 1$ helper(s)	t	p <sup>2</sup>		
MALE BREEDERS						
(a) May–Jul	23.2 $\pm$ 5.2 (4)	23.3 $\pm$ 7.8 (14)	0.05	>0.50	19	−0.18
(b) Aug–Sep	20.6 $\pm$ 4.9 (4)	14.1 $\pm$ 5.3 (6)	1.83	>0.10	10	−0.57
(c) Oct–Mar	48.7 $\pm$ 4.6 (3)	35.9 $\pm$ 6.9 (12)	3.12	<0.01	15	−0.76
(d) Apr–May	17.6 $\pm$ 9.8 (4)	20.1 $\pm$ 6.6 (7)	0.49	>0.50	11	+0.05
FEMALE BREEDERS						
(a) May–Jul	26.2 $\pm$ 8.6 (4)	20.5 $\pm$ 7.3 (14)	1.21	>0.20	19	−0.25
(b) Aug–Sep	14.5 $\pm$ 4.5 (4)	6.9 $\pm$ 4.2 (6)	2.60	<0.05	10	−0.64
(c) Oct–Mar	31.9 $\pm$ 12.0 (3)	26.8 $\pm$ 10.1 (12)	0.73	>0.20	15	−0.05
(d) Apr–May	4.5 $\pm$ 4.1 (4)	11.5 $\pm$ 6.8 (7)	1.68	>0.10	11	+0.43
TOTAL GROUP						
(a) May–Jul	44.6 $\pm$ 8.7 (6)	53.7 $\pm$ 13.7 (14)	1.60	>0.10	20	+0.17
(b) Aug–Sep	36.5 $\pm$ 7.9 (4)	28.8 $\pm$ 7.6 (7)	1.56	>0.10	11	−0.01
(c) Oct–Mar	73.1 $\pm$ 8.5 (3)	73.1 $\pm$ 7.4 (12)	0.004	>0.50	15	−0.17
(d) Apr–May	23.3 $\pm$ 9.2 (4)	42.6 $\pm$ 9.0 (7)	3.24	<0.02	11	+0.71

Period (a) began after fledglings were present or a nest failed, which varied from year to year; generally the division between (d), an active nest, and (a) mid-May

Two-tailed tests on arcsine-transformed data

One-tailed tests

Table 3: Sentinel times for the 10 study groups (study B)

Group name	No. helpers	Total watch (min)	Observation time (min)	Sentinel time (min)	% sentinel time <sup>1</sup>
EBAY	0	624	554	424	76.5
WCPR	0	513	120	90	75.0
RATL	0	597	333	241	72.4
POLA	0	638	234	158	67.5
WCOP	0	611	511	328	64.2
ARCT	1	607	335	223	66.6
SAND	4	600	330	205	62.1
IBRN	2	637	32	14	43.8
SSAN	1	620	509	205	40.3
NWES	1	611	555	210	37.8

<sup>1</sup> 100(sentinel time)/observation time

Results — Study B

Hypothesis 1: Helpers Participate Non-trivially in Sentinel Behaviour

Some background data from Study B are necessary to characterize the degree of participation of helpers. Much of this background is also relevant to the other three hypotheses tested but it seems appropriate to present it all at once in this section. In particular, the data made it clear that sentinel behaviour of helpers cannot simply be compared with ‘breeders’ because male and female breeder often differed. Table 3 shows basic sentinel data from all 10 groups. Seven groups had one or more sentinels for more time than they had no sentinel; the exceptions (groups NWES, SSAN and IBRN) all had one or more helpers.

Bouts of sentinel duty were of random length. Fig. 4 shows log survivorship curves of the length of sentinel bouts for the breeding male and female in the four groups without helpers and with sufficient data: no consistent differences exist between male and female, nor does the number of bouts per unit time differ between the sexes (in all cases the y-intercepts of the curves are approximately the same for male and female). All data conform to exponential decay functions, as shown by the fitted linear-regression lines. The  $r^2$  values are high in all cases; for male and female, respectively: 0.970 and 0.937 (EBAY), 0.975 and 0.972 (POLA), 0.984 and 0.971 (RATL), 0.991 and 0.980 (WCOP), and 0.980 for one female (WCPR, not shown). Therefore, the length of a sentinel bout is random in the sense that a jay has a constant probability of ending sentinel duty regardless of how long it has already been engaged. Furthermore, the conformity to exponential decay specifies the median value as the appropriate measure of central tendency in the distribution of bout lengths; the median is analogous to the half-life of exponential radioactive decay.

Fig. 5 shows similar survivorship curves for the four groups with one or

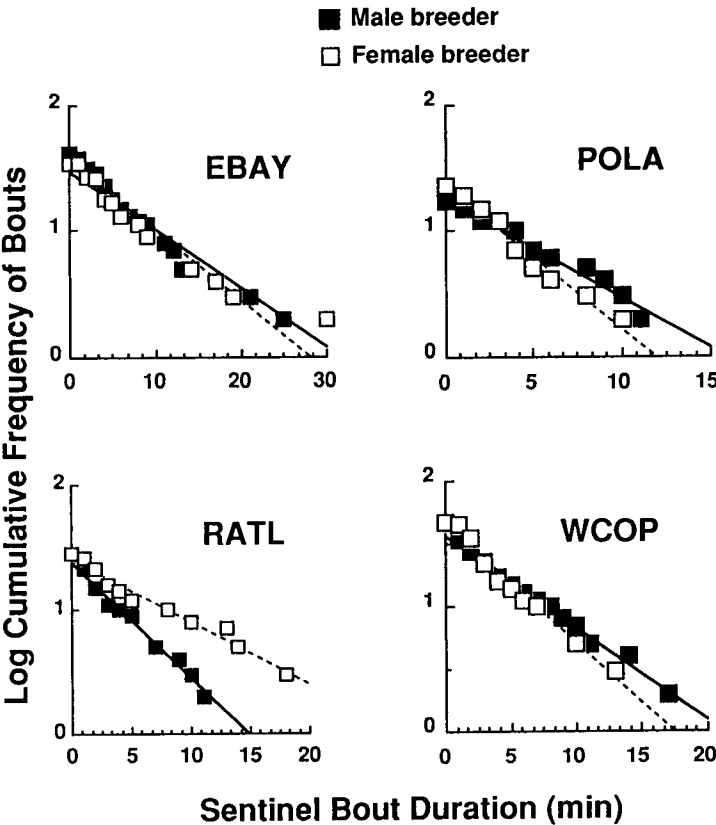


Fig. 4: Common-logarithm cumulative-frequency curves for sentinel bout durations in four groups of study B (Table 3) without helpers (cf. Fig. 5). The conformity to exponential decay means that sentinel bouts are random in length (see text for details, including correlation coefficients)

more helpers and with sufficient data. The points made regarding Fig. 4 also apply here: no consistent differences between male and female breeder, and conformity of curves to exponential decay functions. Helpers participate in sentinel duty, although they perform fewer bouts (y-intercept lower) than that of the male breeder in each case and less than that of the female breeder in all but one group (SAND). Curves for helpers also conform to exponential decay functions, with high  $r^2$  values: 0.965 (ARCT); 0.922 (NWES); 0.965, 0.962, 0.947 and 0.878 (SAND); and 0.938 (SSAN). In the only group with sex comparisons among helpers (SAND), male and female helpers did not differ.

Fig. 6 (left) displays the relative sentinel participation of male and female breeders in groups without helpers. One sex does not consistently participate more than the other as the male's total sentinel time is greater in two groups (POLA and WCOP), the female's in two (RATL and WCPR), with the sexes being about equal in one (EBAY). The number of sentinel bouts by male and female breeders was compared within each group by the two-tailed binomial test,

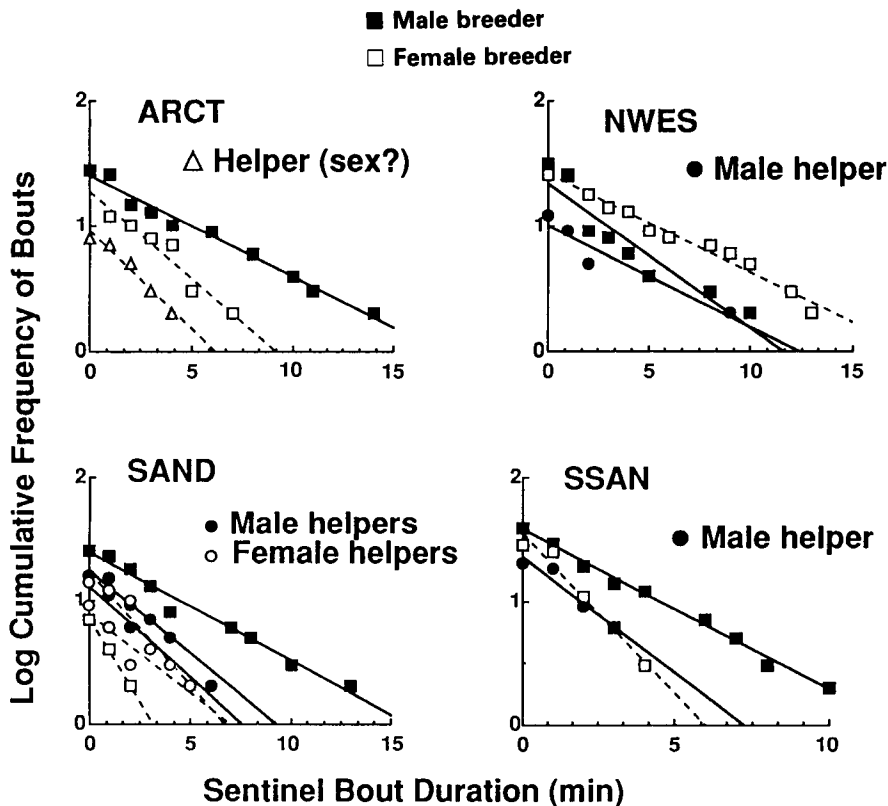


Fig. 5: Common-logarithm cumulative-frequency curves for sentinel-bout durations in four groups of study B (Table 3) having one or more helpers (cf. Fig. 4). All curves show conformity to exponential decay (see text for details, including correlation coefficients)

and only one (WCPR) showed a significant difference (two bouts for male, 16 for female,  $p = 0.0007$ ). However, the male's median bout was 2.5 min whereas the female's was only 2.0 min, and the distributions of bouts did not differ (Mann-Whitney  $U = 13.5$ ,  $p > 0.4$ ). This is the only pair for which a sex-difference might exist, as in all other groups in Fig. 6 the Mann-Whitney  $U$  values were very large ( $p > 0.45$  in all groups).

Fig. 6 (right) also shows data for groups with one or more helpers. In all families (except IBRN, where insufficient data exist) the male breeder spent more total sentinel time than the female breeder. Binomial tests on the number of bouts and Mann-Whitney  $U$  tests on the distributions of bout lengths were run: in no case did the distributions of bout lengths differ ( $p > 0.4$  for all groups), but in two the male carried out more sentinel watches than the female (ARCT: 26 vs. 12,  $p = 0.024$ ; SAND: 23 vs. 4,  $p = 0.0002$ ). These two differences can be seen as differences in the y-intercepts of Fig. 5. The overall differences between male and female breeders in number of bouts as well as total sentinel times were tested

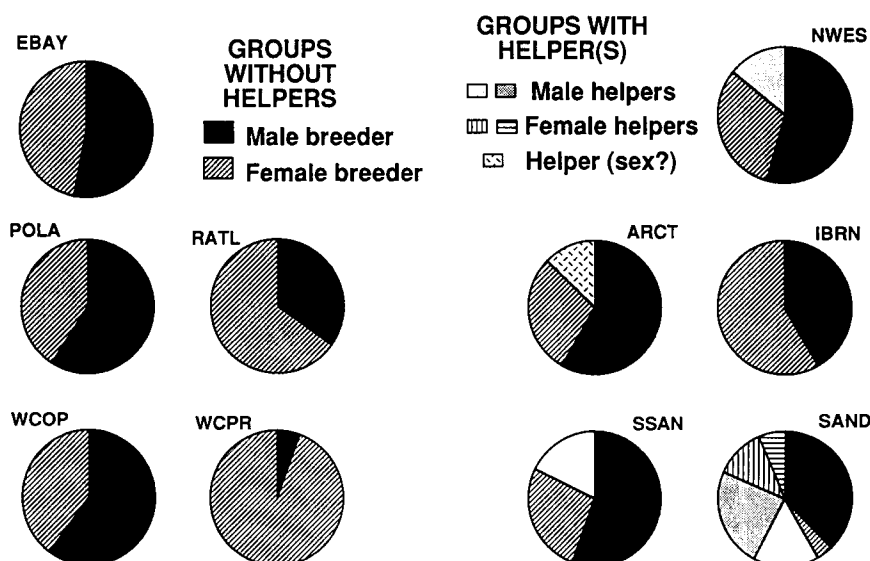


Fig. 6: Proportion of sentinel contribution by sex-age class in study B. Above each pie-chart is given the group name. See text for statistical tests

over all 10 groups, but in neither case was the difference significant ( $p > 0.38$  for number of bouts and  $p > 0.12$  for total sentinel time; Wilcoxon matched-pairs, signed-ranks test).

Helpers participated non-trivially in sentinel behaviour (Fig. 6). The single helper in each of three groups (ARCT, SSAN and NWES) undertook less absolute sentinel time than either breeder. In one (SAND), each of the four helpers undertook less absolute sentinel time than the male breeder but more than the female breeder. Each helper's sentinel duty was compared with that of the two breeders in its group. In no case did a significant difference exist in distributions of bout lengths between any helper and either of the breeders of its group (14 Mann-Whitney U tests,  $p > 0.05$  in all groups). However, some differences occurred in the number of bouts. The male breeder of various groups had significantly more bouts than the helper of unknown sex in ARCT (26 vs. 7,  $p = 0.0008$ ), the male helper in NWES (25 vs. 9,  $p = 0.006$ ), one of the male helpers in SAND (23 vs. 11,  $p = 0.041$ ), and one of the female helpers in SAND (23 vs. 6,  $p = 0.0001$ ). Furthermore, in all seven comparisons the male breeder had absolutely more sentinel bouts than any helper in his group ( $p = 0.008$ , binomial). Comparisons between helpers and the female breeder, however, provide fewer statistically reliable differences. The female breeder in NWES had more bouts than the male helper (26 vs. 9,  $p = 0.004$ ), one male helper at SAND had more bouts than the female breeder (15 vs. 4,  $p = 0.012$ ), and one female helper in the same group had more bouts than the female breeder (12 vs. 4,  $p = 0.049$ ). The results are therefore mixed with regard to degree of sentinel participation of helpers and female breeders.

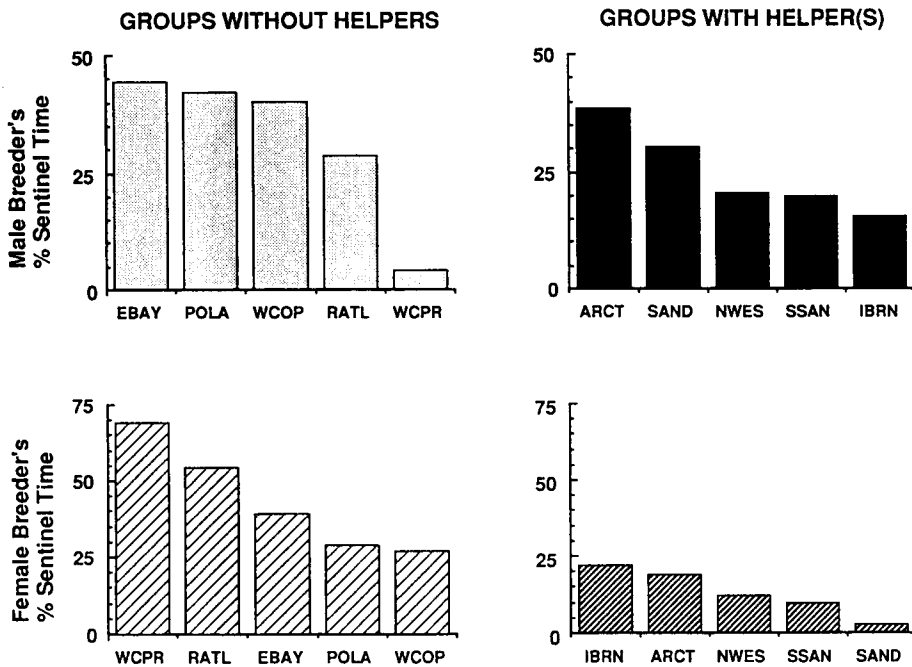


Fig. 7: Comparisons of male (top) and female breeder sentinel time in groups without (left) and with helpers (study B). See text for statistical comparisons

Finally, in the SAND group, it is possible to compare male and female helpers statistically. In the four possible comparisons of distributions of bout lengths, no result was significant according to the Mann-Whitney U test ( $p > 0.45$  for all four comparisons). Only one comparison of number of bouts was marginally insignificant (one male helper 15 bouts vs. one female helper 6 bouts,  $p = 0.052$ , two-tailed binomial).

To summarize, the general result is that all birds of a group, including the helpers, participate in sentinel behaviour and do so nearly equally. Some statistically reliable evidence suggests greater participation by the male breeder than the female breeder, but it is neither large nor consistent among groups. Still stronger evidence supports a tendency for male breeders to participate more than helpers of either sex, but female breeders and helpers have no consistent difference in participation among groups. Finally, no difference in participation can be established between sexes of helpers at this time of year.

### Hypothesis 2: Helpers Decrease Sentinel Time of Breeders

Fig. 7 compares sentinel times as a percentage of the total time the group was under observation for both breeders in all groups. In every group with helpers (upper right) the breeding male spent less time on sentinel than the median sentinel

time of male breeders in groups with no helpers (upper left). The trend is thus in the predicted direction, with median percentages of 40.1 % for male breeders without helpers and 20.5 % for male breeders with helper(s); however, the Mann-Whitney U test of the difference is not significant ( $n_1 = n_2 = 5$ ,  $U = 7$ ,  $p = 0.31$ ).

The lower part of Fig. 7 shows that the difference is much stronger in the female breeders, with every female breeder in groups with helper(s) having spent less time on sentinel duty than the female with the lowest sentinel time (WCOP) in groups without helpers. The median percentages were 39.4 % for female breeders without helpers and 12.1 % for those with helper(s), and this difference is statistically reliable ( $n_1 = n_2 = 5$ ,  $U = 0$ ,  $p = 0.008$ ). Stated the other way around, this result shows that female breeders with helpers have more available foraging time because they spend less time on sentinel duty. The same non-significant trend can be seen in male breeders.

### Hypothesis 3: Helpers Increase Guarded Foraging Time of Breeders

Put operationally, the total observation time of a breeder is divisible into three categories: 1. On sentinel duty; 2. Not on sentinel duty and no one else on sentinel duty; and 3. Not on sentinel duty but some other group member on sentinel duty. It is the last component, expressed as a percentage of the total observation time, that was posited to increase because of helper participation in sentinel behaviour.

Fig. 8 shows that the results were not at all in accordance with the hypothesis. In the upper half of the figure it can be seen that male breeders in groups with helpers (right) tended to have less, not more, absolute 'protected' foraging time than the median male in lone pairs (left). The median values were 57.8 % for male breeders without helpers and 33.3 % for those with helpers, a difference that is large but not significant using the Mann-Whitney U test ( $n_1 = n_2 = 5$ ,  $U = 4$ ,  $p = 0.096$ ).

The lower half of Fig. 8 suggests the same trend, but with no clear difference between female breeders with and without helpers ( $\bar{x} = 51.1$  % and 33.9 %, not significant:  $n_1 = n_2 = 5$ ,  $U = 11$ ,  $p = 0.84$ ). Therefore, no statistically established difference exists in 'protected' foraging time for breeders both with and without helpers.

### Hypothesis 4: Groups with Helpers Display Greater Total Sentinel Time

The foregoing results indicate that helper participation does not compensate for the decrease in sentinel time by the breeders. Therefore, the total sentinel time (all birds combined), expressed as a percentage of total observation time, was compared between groups with and without helpers. Fig. 9 shows that total sentinel time in all groups with helpers is less than all but the least sentinel time for groups without helpers (WCOP). The median percentage sentinel time in lone pairs was 72.4 % compared with 43.8 % in groups with helpers, a significant difference according to the Mann-Whitney U test ( $n_1 = n_2 = 5$ ,  $U = 1$ ,  $p = 0.016$ ).



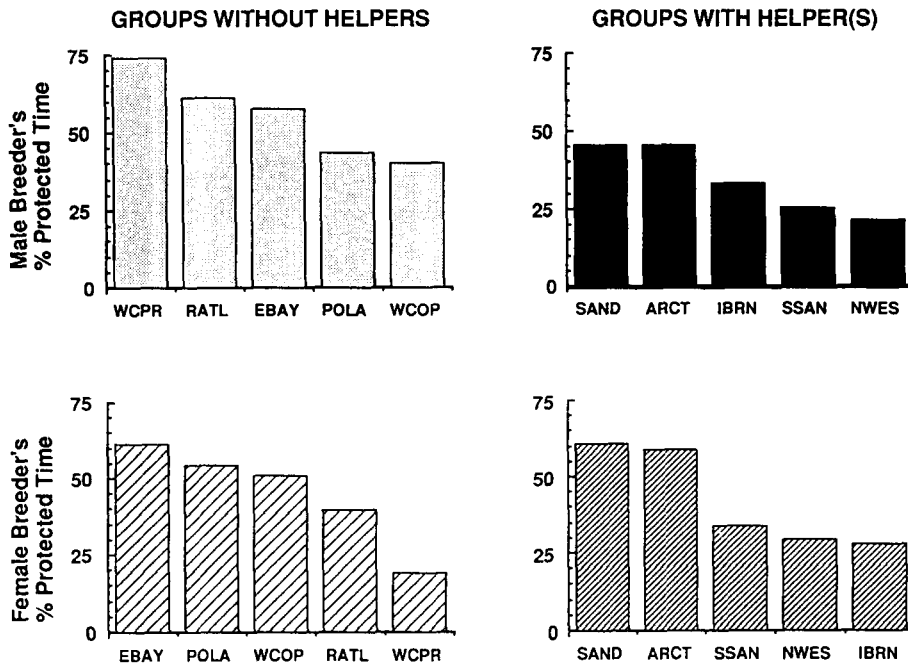


Fig. 8: Comparisons of male (top) and female breeder 'protected' available foraging time in groups without (left) and with helpers (study B). For statistical comparisons, see text

## Discussion

### Comparisons between the Two Studies

It is rare to have two behavioural studies using somewhat different methods directed toward the same set of questions on the same animals. We here compare the three most important aspects of the results.

*Sentinel participation by group members.* Both studies found that, by Jan., virtually all members of jay groups, including any birds hatched the previous summer, participated in sentinel behaviour. Both studies found that the male breeder tended to spend more total time on sentinel duty than any other group member, and also tended therefore to have the greatest share of sentinel duty, although this trend was not consistent in every group. Both studies also found that the female breeder, on average, spent the second-most amount of time and the second-greatest percentage of sentinel duty in a group, but this result was even less consistent than the male's first place. Neither study could statistically establish any sex difference in helpers with regard to sentinel-performance measurements in winter, although study A did find significant differences during the nesting period (not covered by study B).

*Comparisons of breeders with and without helpers.* Both studies found that male breeders with helpers spent less absolute time on sentinel duty than those

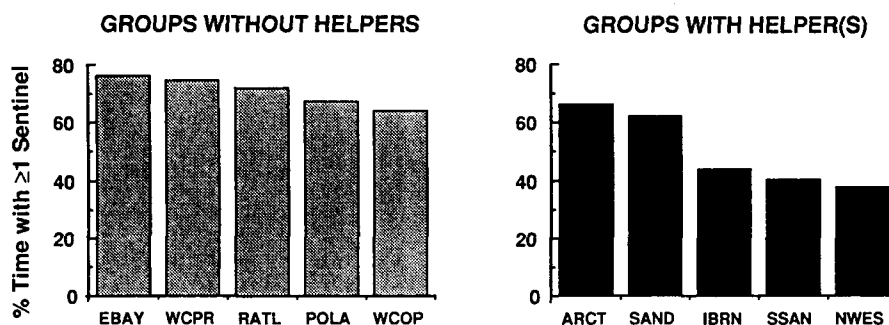


Fig. 9: Comparison of total sentinel time in groups without (left) and with helpers (study B). See text for statistical comparisons

without helpers; the difference was statistically significant in Study A but not in Study B. Both studies also found that the female breeders with helpers spent less absolute time on sentinel duty than those without helpers; in this case the result was not significant in Study A but was significant in Study B. Study A found that breeding males in families with helpers had more available protected foraging time, whereas Study B found no significant difference, but with trends in the opposite direction.

*Comparison of total sentinel time in groups with and without helpers.* The only other directly comparable results concern total sentinel time. Study A found no difference between groups with and without helpers, and in fact the mean percentages of time spent on sentinel duty were identical (73.1 %). Study B, however, found a difference, lone pairs having a sentinel for an average of 72.4 % of the time but groups with helpers for only 43.8 % of the time (statistically significant). Whatever the cause of the different results, it has no effect on the conclusion. The research hypothesis was that groups having helpers would have a greater percentage of their time covered by at least one sentinel on duty; study A found no difference and study B found a difference in the opposite direction, so both studies reject the hypothesis.

In general, the two studies agreed on all major points and differed only in details. Discrepancies could result from many factors, among them the difference in study period (Oct.–Mar., study A; Jan., study B), and differences in sample sizes (three groups without helpers and 12 with, study A; five of each, study B).

### Sexual Asymmetries

We found that male breeders tend to participate in sentinel behaviour more strongly than females, although there were groups in which the reverse was true. Sexual asymmetries in a monomorphic species, especially during the non-breeding season, may seem surprising but many behavioural differences have been documented in the Florida scrub jay (WOOLFENDEN & FITZPATRICK 1986; FRANCIS et al. 1989). The present study establishes some quantitative differences in sentinel

behaviour. Male breeders tend, on average, to participate more than female breeders. In groups with helpers, the male always had greater sentinel participation.

Behavioural asymmetries between the sexes are less noticeable among helpers, but some may occur (FRANCIS *et al.* 1989; MCGOWAN 1987). In the present study of sentinel behaviour, the participation by male helpers was usually absolutely greater than that by female helpers of the same age class, although the difference was rarely significant. The only consistently significant differences between helpers were during nesting, when females performed more sentinel duty. As noted above, during nesting, the reverse tends to be true for breeders, males performing more sentinel duty than females. We suggest that this reversal reflects division of labour by breeders. Females have a drive to sit on the nest, but female helpers are kept from doing so by the breeders (STALLCUP & WOOLFENDEN 1978; WOOLFENDEN & MCGOWAN unpubl. data). Female helpers may spend time near the nest as a reflection of this drive, and, while there, act as sentinels. Male helpers lack such a drive, and spend their time gathering food to feed the nestlings, similar to the actions of the breeding male. STALLCUP & WOOLFENDEN (1978) found that male helpers fed nestlings more than female helpers of the same age.

#### Effect of Helper Sentinel Behaviour on Breeders

In light of the results, how might helper sentinel behaviour contribute to the known higher survival of breeders with helpers? An unlikely possibility is that helpers could be better at watching for raptors than are breeders. If so, helper substitution for breeder sentinel behaviour might contribute to better breeder survival. Such an argument seems far-fetched in light of MCGOWAN's (1987) findings that inexperienced birds often give false alarms to non-dangerous stimuli and appear not to be 'trusted' with the responsibility of sentinel duty by the breeders.

At the other end of the spectrum of logical possibilities is helper hindrance. No evidence exists from any field observations that helpers physically or behaviourally in any way inhibit breeders from standing sentinel. However, breeders might 'assume' someone else is on sentinel duty, and hence decrease their own sentinel time when helpers are a part of the group. Perhaps more likely is that with three or more members in a group, foragers may delay in beginning sentinel duty — either because they are 'unsure' if another bird will do it, or because if they delay another may do it. The effect might be something like people fumbling for their wallets when a restaurant bill is delivered. With merely a breeding pair, when the mate leaves the sentinel post the foraging bird knows it should stand sentinel because there is no other bird to do so.

A third interpretation is that formal sentinel watch becomes less necessary in groups with helpers. Sentinel duty may also be more difficult to coordinate in larger groups. During the fall-winter period, study A found a significant negative correlation between group size and the amount of sentinel behaviour by male breeders, and a similar result occurred during the Aug.–Sep., period. The winter correlation was also negative with female-breeder sentinel time during these two periods, but significant only during the Aug.–Sep. period. All the results we have

collected are consistent with the interpretation that it is not specifically the sentinel behaviour of helpers that makes breeders decrease their own sentinel behaviour, but rather the mere presence of helpers. Therefore, we propose that additional pairs of eyes and ears constitute sufficiently increased predator protection; increased formal sentinel duty is unnecessary. Our observations agree with results of the many empirical studies cited in the introduction and with the prediction of WARD (1985) that the benefits of coordinated vigilance decrease as group size increases.

The potential contribution of helper sentinel behaviour to the known higher reproductive success of breeders with helpers seems more straightforward. During this period, total group sentinel coverage is higher when helpers are present. As groups tend to forage in the vicinity of the nest, sentinels are helping to protect other birds and the nest contents simultaneously.

### Comparisons with Other Studies

Studies of vigilance in other cooperative breeding species have found results similar to this study: older adults, especially breeders, tend to be more vigilant than younger group members (GASTON 1977; FERGUSON 1987; HEINSOHN 1987; ZAHAVI 1990). RASA (1986), however, found that subordinate-male dwarf mongooses (*Helogale undulata*) were more vigilant than any other class. As in our study, FERGUSON (1987) found that total vigilance did not differ between large and small groups in white-browed sparrow-weavers (*Plocepasser mahali*). ZAHAVI (1990) treated sentinel behaviour in Arabian babblers (*Turdoides squamiceps*) as a display by which group members could show their status. The alpha male in a breeding group performed the most sentinel duty, others competed to act as sentinels, and subordinates refrained from replacing a dominant. We made our observations in the same fashion as ZAHAVI and found no aggressive interactions among individuals likely to be involved in a dominance struggle. Although sex is the strongest determinant of dominance in Florida scrub jay groups (all adult females being subordinate to all adult males; WOOLFENDEN & FITZPATRICK 1977), we found little consistent difference according to sex in sentinel behaviour; age has a stronger predictive effect. Therefore we find no evidence to support ZAHAVI's hypothesis.

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