

FIGURE 2. Sound spectrograph of male position note of Pacific-slope Flycatcher from Sierra Laguna, Baja California Sur.

(1980) in southeastern Arizona (Table 1), although the frequency spread of the descending portion (part 2) of syllable 2 is much narrower. Thus, Cordilleran Flycatchers in southern Mexico seem closely allied by song-

type to those 1,200 km to the north in the interior southern United States, and their advertising songs show little gradation toward the songs given by the Yellowish Flycatcher (*E. flavescens*, Johnson 1980:fig. 27), a sibling species breeding as close as 500 km to the Hidalgo site. Recordings of advertising songs of Cordilleran Flycatchers from Oaxaca and of Yellowish Flycatchers from southeastern Veracruz or southeastern Oaxaca, i.e., where these species' ranges approach most closely, would further clarify this situation (Johnson's northernmost recordings of the latter species came from Nicaragua).

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## THE INFLUENCE OF GROUP SIZE ON VIGILANCE IN CAPTIVE-RAISED RING-NECKED PHEASANTS<sup>1</sup>

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Two of the main environmental influences on the evolution of animal aggregations are thought to be food availability and predation pressure (Bertram 1980). Group formation is hypothesized to be a means by which individuals can exploit uneven food supplies

(e.g., information-transfer; Ward and Zahavi 1973), minimize the risk of predation through dilution (Hamilton 1971), or increase group vigilance (Abramson 1979). These ideas have been used to explain the function of groups in many different animals, e.g., communal roosts of birds (Weatherhead 1983), fish schools (Brown and Downhower 1988), and maternity colonies of bats (Kunz 1982).

Evaluating the function of aggregations should provide insight into the degree of food availability and predation pressure to which an animal is subjected. For example, Bertram (1980) showed that although individual Ostriches (*Struthio camelus*) spent less time scanning when in groups, overall vigilance (proportion of time when at least one bird scanned) increased with group size. If, by being in larger groups, individual

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animals are able to spend less time watching for predators, more time should be available for mutually incompatible activities such as foraging. An increase in the amount of time available for feeding and a decrease in risk of predation will tend to increase the survivorship of an individual, a combination that should be favored by natural selection.

Under natural conditions, Ring-necked Pheasants (*Phasianus colchicus*; henceforth "pheasants") typically form groups of three or four birds of mixed age and sex (Hill and Robertson 1988), with females tending to group more than males. In recent years an increasing number of captive-raised pheasants have been released into the wild for sport hunting in Britain and North America. Released birds appear to suffer higher mortality than wild individuals (Hill and Robertson 1988). Hill and Robertson (1988) suggested that underdeveloped anti-predator behaviors in hand-reared pheasants may account for this. They hypothesize that effective anti-predator behaviors do not develop in hand-reared pheasants as well as wild pheasants because of a lack of reinforcement provided naturally by the hen. Individuals of most wild bird species studied to date are less vigilant in larger groups (e.g., Caraco 1979). We predicted that hand-reared pheasants placed into different group sizes would not display vigilance behavior typical of most wild bird species. In particular, we predicted that captive-raised pheasants would not vary vigilance with changes in group size.

## METHODS

Data were collected on the vigilance behavior of pheasants housed in an outdoor aviary 28 km north of Regina, Saskatchewan, between 21 October and 25 November 1990. Wild pheasants were abundant in the surrounding area which consisted of small valleys with deciduous trees and shrubs. The 3 m high aviary was constructed of 2 cm poultry mesh on the tops and sides, and was divided into a 14 × 10 m observation section and a 28 × 10 m holding section. The birds consisted of several subspecies that are not easily distinguished (Hill and Robertson 1988). To control for possible effects of sex and age on vigilance, we used 12 adult, 1.5 year-old females in the experiments. A 1.3 m high opaque barrier was erected between the two sections to restrict visual interaction between birds in the holding section and the experimental subjects. Vocalizations were noted, but no attempt was made to eliminate or hold them constant.

Individual vigilance was recorded for experimental group sizes of solitary pheasants or groups of either four or 10. Each group size was observed on three randomly chosen days. Experimental birds were placed in the observation section of the aviary the night before observations were made. Birds used solitarily or in groups of four individuals were randomly chosen from the 12 birds available, provided they had not been observed previously in that particular group size. For observation sessions involving 10 birds, we randomly selected 10 of the 12 available females.

Vigilance was recorded using focal animal sampling (Lehner 1979). Individuals were observed for 5 min during 2 hr sampling periods in the morning, middle afternoon, and late afternoon. The morning sampling

period always began between 09:30 and 10:00, the mid-afternoon period at 12:30, and the late-afternoon period at 15:00. During each sampling period, we recorded vigilance during 12.5 min intervals. Thus, vigilance of each individual in groups of one, four, and 10 was recorded 12 times, three times, and once, respectively, during each 2 hr period. All observations were made from within the aviary. If birds moved behind an obstruction, observations were halted until the focal bird reappeared. The pheasants stopped foraging each time an observer entered the aviary, but they resumed foraging within a few minutes. To acclimate birds to our presence, we waited inside the aviary for 30 min before beginning each sampling period. If birds were disturbed by any extraneous variables (e.g., dog or horse), observations were halted for 30 min. In total, we completed 362.5 min samples.

We recorded the amount of time each bird spent with its long axis (imaginary line running through the head and neck) below an angle parallel with the ground, with the anterior end lower (henceforth "head down"), and the number of times each bird put its head down. Amount of time spent with head down was used as an indicator of time not spent vigilant. Scanning and feeding were by far (>95% of time) the most commonly observed behaviors.

Temperature and food availability can affect vigilance. For example, mean size of sparrow flocks has been shown to vary inversely with both temperature and food availability (Caraco 1979). In order to minimize weather effects on vigilance, all observations were made on sunny or partly cloudy days when minimum temperature was greater than -15°C the previous night. Temperatures were recorded before each sampling period using a max-min thermometer mounted at ground level. To control for effects of food availability, we distributed grain ad lib throughout the observation area of the aviary before each day of observations.

The effects of group size and time of day of sampling period on mean vigilance (mean time spent with head down and mean number of times with head down) were analyzed using a two-way repeated measures ANOVA with an incomplete block design (Wilkinson 1990). If a significant effect was found among the levels of a factor, a Tukey's test was used to make pairwise comparisons (Zar 1984). For all statistical tests the null hypothesis was rejected when  $P < 0.05$ .

## RESULTS

Time of day had no significant effect on the mean number of times a focal bird put its head down (ANOVA  $F = 0.407$ ;  $df = 2, 43$ ;  $P > 0.50$ ) or the amount of time spent with head down (ANOVA  $F = 0.065$ ;  $df = 2, 43$ ;  $P > 0.50$ ). However, group size did have a significant effect on both the mean number of times with head down (ANOVA  $F = 56.983$ ;  $df = 2, 43$ ;  $P < 0.001$ ; Fig. 1) and the amount of time spent with head down (ANOVA  $F = 171.750$ ;  $df = 2, 43$ ;  $P < 0.001$ ; Fig. 1). The interaction between time of day and group size was not significant for either the mean number of times with head down (ANOVA  $F = 0.159$ ;  $df = 4, 43$ ;  $P > 0.50$ ) or the amount of time spent with head down (ANOVA  $F = 0.389$ ;  $df = 4, 43$ ;  $P > 0.50$ ).

There was a significant difference in the mean num-

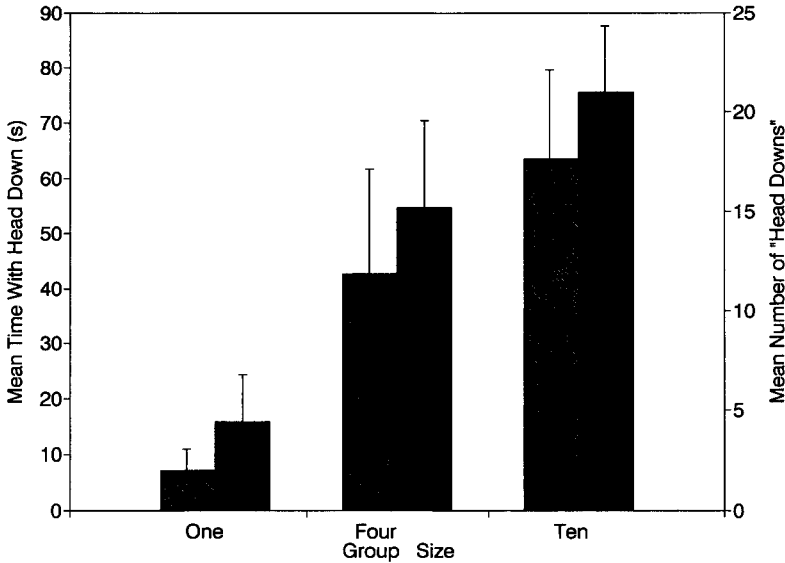


FIGURE 1. Means and standard errors for number of times (solid bars) and amount of time (diagonal lines) individual pheasants put their head down per 5 min period when they were tested solitarily and in groups of four and 10 individuals.

ber of times pheasants put their head down when they were solitary versus in a group of four individuals (Tukey's  $q = 11.867$ ;  $df = 3, 49$ ;  $P < 0.001$ ), when solitary versus in a group of 10 (Tukey's  $q = 17.496$ ;  $df = 3, 49$ ;  $P < 0.001$ ), and when in a group of four versus 10 (Tukey's  $q = 8.930$ ;  $df = 3, 43$ ;  $P < 0.001$ ). Likewise, there was a significant difference in amount of time pheasants spent with head down when solitary versus in groups of four (Tukey's  $q = 19.976$ ;  $df = 3, 49$ ;  $P < 0.001$ ), when solitary versus in a group of 10 (Tukey's  $q = 29.334$ ;  $df = 3, 49$ ;  $P < 0.001$ ), and when in a group of four versus 10 (Tukey's  $q = 14.864$ ;  $df = 3, 49$ ;  $P < 0.001$ ).

During the experiment, possible anti-predator behaviors, other than vigilance, were also observed. Female pheasants were observed to give calls that were immediately followed by birds in both sections of the aviary standing still and scanning. On several other occasions, a farm dog approached the aviary and the pheasants either ran or flew away from the dog. The birds remained vigilant for several minutes after the dog left. On one occasion a Marsh Hawk (*Circus cyaneus*), flew over the aviary and the pheasants went to cover or quickly laid down with their heads covering their brightly colored chests. In this case (individuals in a group of four), the focal birds did not return to active foraging for more than 30 min.

#### DISCUSSION

We found that both the number of times an individual pheasant put its head down to feed and the amount of time that an individual spent with its head down varied inversely with group size. Individual vigilance decreased between individuals observed in groups of four and individuals observed solitarily. These results indicate that hand-reared pheasants facultatively adjust

their vigilance level in response to group size. The decrease in vigilance in pheasants in larger groups is similar to patterns of vigilance behavior found in wild birds (e.g., Bertram 1980, Studd et al. 1983). However, comparisons with wild pheasants cannot be made because vigilance behavior, with respect to variation in group size, has not been studied to date.

Pulliam (1973) proposed a mathematical model suggesting that the probability of detecting a predator levels off very quickly as flock size increases. This suggests that there is a critical point at which predators are easily detected and an increase in group size should no longer affect individual vigilance behavior. For example, individual vigilance by curlews (*Numenius arquata*) does not decrease in flocks of more than six birds (Abramson 1979) or in flocks of House Sparrows (*Passer domesticus* L.) of more than five birds (Elgar and Catterall 1981). The small number of group sizes studied do not provide an indicator of possible leveling off of individual vigilance.

Birds may decrease vigilance by reducing either the duration or frequency of scanning. Reduction in scan duration, but not scan frequency, has been found in White Storks (*Ciconia ciconia*; Carrascal et al. 1989) and house sparrows (Studd et al. 1983). Our results show that the total amount of time spent with the head down increased with the rate at which the head was put down. Therefore, captive-raised pheasants decreased their vigilance with increased group size by reducing both the scanning frequency and scan duration.

In this study, food availability was high and observations were made only on days with similar climatic conditions. There is likely a tradeoff between vigilance and foraging, so when food is superabundant there is little cost to increasing vigilance time. Thus, in our

study, any adjustment in vigilance level must have been in response to factors other than food availability.

Vigilance patterns might be affected by the presence of individuals of different ages or sexes (e.g., Waite 1987), a factor we did not consider. In larger flocks, subordinates might face a time constraint with respect to meeting their energy intake requirements because higher-ranking conspecifics interfere with their foraging (e.g., Knight and Knight 1986). Therefore, we would expect subordinate birds to be more vigilant. However, further investigation is required to determine if individual differences in vigilance among pheasants are related to age, sex, dominance status, or captive versus wild status.

The patterns of vigilance, apparent warning calls, and responses to different predators we observed indicate that captive-raised Ring-necked Pheasants possess potential anti-predator behaviors. We conclude that heavy mortality of released captive-raised pheasants into the wild is not solely because they lack such behaviors. But we still need to know if vigilance behaviors are as well developed in captive as in wild birds. We suggest a similar study in which the vigilance behavior of a larger number of captive-raised birds is compared with that of wild pheasants after they've been released.

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