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Age-related Spatial Segregation of Great Cormorants in a Roost

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Abstract.—Agonistic interactions between Great Cormorants (*Phalacrocorax carbo*) in a roost have been studied to detect possible social dominance causing spatial segregation in relation to age. Adults tended to dominate first- and second-winter birds, and were found relatively higher in the roost, where they are probably the safer from human intruders. Because of the high proportion of adults, attacks frequently involved two adults. No differences were found between the frequency and success of attacks in relation to the age of the birds arriving to the roost, perhaps indicating that pre-attack display represented an efficient form of agonistic communication. The number of attacks was not correlated with the number of cormorants in the roost, probably due to a constant density of birds, unaffected by the size of the roost. *Received 17 September 2003, accepted 10 July 2004.*

Key words.—Age classes, agonistic interaction, Great Cormorant, *Phalacrocorax carbo*, social dominance, spatial segregation.

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Several features of communal roosting in birds may provide adaptive benefits. Advantages of communal roosting that are commonly mentioned include: (1) reduction of energetic demands for thermoregulation; (2) predation avoidance, by a dilution effect or by the geometry of the groups; and (3) increase in the foraging efficiency by acting as information and recruitment centers at the roost and food patches (Beauchamp 1999 and cited references).

On the other hand, communal roosting has costs associated with the spatial competition for the better sites, due to the following factors: (1) birds located at the poorer sites in the roosts have a higher predation risk (Ekman 1987); (2) the size of the defended site in the roost is negatively correlated with the intruder pressure, indicating that the cost of the territory defense increases with the bird density (Ewald *et al.* 1980); and (3) adverse meteorological conditions increase the physiological cost of thermoregulation in the birds located at the worse sites of roosts in trees (e.g., Swingland 1977; Yom-Tov 1979).

The Great Cormorant (*Phalacrocorax carbo*) normally roosts communally and Lekuona (2000) found that adults were dominant over first and second year birds in the spatial competition. This dominance of older cormorants has been also observed in acts of kleptoparasitism (Lekuona and Campos 2001), although the consequences of this social dominance have not been studied inside a roost.

The study of spatial segregation in wintering roosts could help in understanding the selective pressures causing their and how the cohesion of the communal roosts is maintained spite of the costs for the subdominant individuals (Beauchamp 1999).

The aim of this study was to determine the existence of possible spatial segregation caused by a social dominance between age classes in the Great Cormorant at a winter roost and to measure the intensity of the attacks that may cause the social dominance.

The following hypotheses were examined: (1) the adult dominance (Lekuona 2000; Lekuona and Campos 2001) will allow these individuals to accede to the better sites of the roost; (2) the adults will instigate a higher number of attacks than subadults due to their defense of the better sites; and (3) the frequency of attacks should be density-dependent (Krebs and Barnard 1980; Lekuona and Campos 2001).

STUDY AREA AND METHODS

The study was carried out in October and November 2002 in a roost of the Great Cormorant in Badajoz (SW Spain, 38°53'N, 06°58'W). The roost was situated on an islet in the Guadiana River in Eucalyptus (*Eucalyptus camaldulensis*) trees almost total lacked leaf cover. This roost is only used in winter.

The roost was visited weekly and observations made over the three hours prior to sunset of the number of birds in the roost and to detect agonistic interactions. The roost was divided in three height zones (low, medium and high) using features of the trees in the roost as reference points and which remained unaltered during the study period.

The birds were divided in three age classes (adult, second winter and first winter; Cramp and Simmons 1977), which were identified by the plumage characteristics, first winter birds had white breasts, and second winter birds had the plumage characteristics intermediate between first winter and adult with the breast mottled white (Van Eerden and Munstermann 1995; Harrison 1996).

In the study of agonistic interactions, birds were observed when they entered the roost. Only cases where there was an agonistic interaction initiated by a bird already present in the roost were recorded. The bird that entered the roost was called the *arriver* and the bird that was initially on the perch and attempted to resist the arriver was called the *incumbent*. For each observation the ages of the incumbent and of the arriver were noted, as well as the result of any attack. An attack was considered successful if the arriver was displaced from the site where it landed, and was unsuccessful when, in spite of receiving an attack, the arriver was able to remain at the site of landing.

Direct counts of the number of birds of each age class in the three height zones of the roost were made at the end of the observation period on each visit, when no more cormorants were entering the roost. Although the number of cormorants at the roost increased during the time when observations were being made, most cormorants had already arrived at the roost at the beginning of the observation period. Therefore, the number of cormorants recorded at the end of the observation period was considered meaningful measure of those capable of making attacks.

Data were normal distributed and parametric statistics were used (Sokal and Rohlf 1995). To test the different frequencies, G-tests based on the number of cormorants and on the number of attacks were carried out, applying the Williams' correction in the single-factor analysis. The proportions of adults, first and second winter birds were used to calculate the expected frequencies of attack made by each age class. Because there were relatively few first and second winter birds, and their behavior was not significantly different, they have been pooled into a single group for analyses of aggressive behavior. Pearson correlation was used to examine possible relationship between the total number of attacks and bird number. ANOVA was used to compare the means of the number of birds of each age class during the study period (Zar 1999).

RESULTS

Description of Attacks

When a cormorant showed intention of flying into a particular part of the roost, the birds already installed defended their perch and warned the intruder by adopting a "wing-waving" posture (Kortlandt 1995). This posture is also used in the breeding colonies as a courtship display to attract females and to claim the possession of the nest (Kortlandt 1995; Lekuona 2000). Although Kortlandt (1995) concluded that the "wing-waving" display was not used in agonistic interactions, it was used here. The head was kept over the back and repetitively moving the wing tips forwards and backwards, maintaining the primary feathers behind the secondaries, thus generating a greater impression of size. If this display was not sufficient to deter the entry of an intruder to a perch, agonistic interactions occurred if it perched within 1m of an incumbent bird. Calls were made only when the arriver was being attacked or near the incumbent. Incumbents did not abandon their perch to carry out attacks.

Age-related Behavior

During the study period, adults were far more numerous than first- and second-winter birds (adults: 71.2% ± 3.9%, Second-winter: 15.0% ± 2.6%, First-winter: 13.9% ± 1.7%; Fig. 1).

Adult cormorants dominated in all three height zones ($F_{2,71}$ = 89.1, P < 0.0001; Table 1) but formed only 60% of the birds in the low zone and increased progressively to almost 79% in the high zone ($F_{2,21}$ = 6.2, P < 0.01, Table 1). There was no difference in the vertical distribution of first ($F_{2,21}$ = 0.54, n.s., Table 1) and second-winter birds ($F_{2,21}$ = 0.08, n.s., Table 1). A total of 315 attacks were observed and these had a 78% success rate for the incumbent (Table 2). The adults made 83% of all attacks, which is 12% higher than their proportion in the roost (Table 2), and were also more successful in their attacks than immature birds (G_2 = 28.7, P <

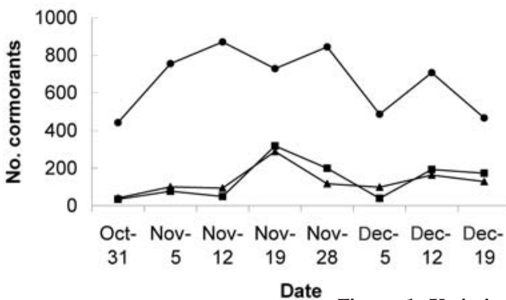

Figure 1. Variation of the total number of adults, second winter and first winter Great Cormorants in the roost during the eight weeks of study. Circles: adults. Squares: second winter. Triangles: first winter.

0.001, Table 2). However, there was no significant difference in the outcome of attacks received by the arrivers in relation to age classes (G_2 = 2.80, n.s., Table 2). Interactions between two immature birds occurred at a level expected by chance, but the cases of an immature bird arriving and being shown aggression by an adult (61 cases) was significantly greater than an arriving adult being threatened by an immature bird (24 cases). The most common interaction (63%) was between two adults.

No significant correlation was found between the total number of attacks and the number of cormorants in the roost (r_6 = -0.40, n.s., Fig. 2).

DISCUSSION

Numerous studies have shown the determining role that sex, age and body size have in the establishment of a social hierarchy (Matthysen 1990). Such a hierarchy permits dominant individuals to have greater access to resources and also to observe groups formed with a greater proportion of dominant individuals at sites that offer limited resources (e.g., Monaghan 1980). In this case and considering only age, the proportion of adults was considerably greater than that of second- and first-winter birds, suggesting that adults of Great Cormorant belong to the higher class in the social hierarchy, as has been found in other studies (Lekuona 2000 and cited references). Although the role of sex must be important because the greater body size of the males would affect these positively in the case of aggression (Fretwell and Lucas 1970), it appears that dominance can be detected considering only age (Lekuona 2000; present study).

Within the roost, adults showed a preference for the highest sites, while second- and first-winter birds had a complementary distribution. The cause of this segregation must be the dominance of the adults, because there is no evidence that subadult birds arrive later at the roosts each day (Lekuona 2000; pers. obs.). Ekman and Askenmo (1984) obtained similar results in Willow Tit (*Parus montanus*) flocks, where dominant adults excluded subordinate juveniles from upper portions of trees in winter. In this species, Ekman (1987) found that the relative proportion of time spent alert increased downwards, suggesting that high positions in trees (pine) are safer than lower zones because there is a higher exposure following from the paucity of living branches in pine trunk portions. The results obtained here are in agreement with this safety-related behavior, but the explanation may be different. Although the Great Cormorant roost has an almost total lack of leaf cover, the youngest trees, located at the low zone, still retain living leaves. Because of this, the birds located there are not in more open positions than birds in upper positions. Small fishing and sport boats were often observed on the river, and when they approached the roost all the cormorants flew away. It seemed to be the principal predation risk posed to the cormorants. No other mammalian predators were seen near the roost. Therefore, the high positions are probably preferred in order to avoid humans.

That first- and second-winter birds were not found with greater frequency in the low-

Table 1. Mean numbers (±S.E.) of Great Cormorants of different ages in the roost zones during the study period (N = 8).

Zone	First winter	Second winter	Adults
Low	53.5 ± 14.9	51.0 ± 20.0	155.8 ± 28.7
Medium	38.9 ± 13.2	44.1 ± 9.3	218.9 ± 25.3
High	36.8 ± 8.3	44.3 ± 8.0	288.6 ± 25.7

Table 2. Number of attacks initiated on Great Cormorants of different ages and corresponding success rate of incumbent.

	Incumbent					
	First and second winter		Adult		Total	
Age of arriving bird	No.	% success	No.	% success	No.	% success
First and second winter	30	57	61	89	91	78
Adult	24	67	200	79	224	78
Total	54	61	261	81	315	78

est zone of the roost could be related to the fact that in social species an effective agonistic display does not cause the retreat of subordinate individuals, but permits the dominant bird to utilize the resource; it is irrelevant to the dominant bird if a subordinate also uses it or not (Senar 1994).

As expected, adult birds attacked more often and had greater success than first- and second-winter birds, and this is in agreement with the results of Lekuona (2000). Studies of kleptoparasitism have shown similar results, where adults had greater success because of their greater experience and power, in Great Cormorants and other species (Burger and Gochfeld 1979; Hesp and Barnard 1989; Reymond and Zuchuat, 1995; Lekuona and Campos 2001; Galván 2003).

No differences were found between the frequency and success of attacks received in relation to age, which suggests that the pre-attack display represents an efficient form of agonistic communication. Thus, the adult plumage must be an honest signal able to prevent these birds becoming victims of greater numbers of attacks in defense of the best roosting sites. This agrees with the results obtained by analysis of aggression frequency after taking into account the ages of arrivers and incumbents. The most frequent situation involved two adults, which indicates that aggression only took place when two birds of similar experience were involved. The greatest level of success found in attacks by adults over individuals of any age is probably related to the greater experience of the adults (Burger and Gochfeld 1979; Hesp and Barnard 1989).

Contrary to expectations, relating the number of attacks with the number of birds present in the roost did not reveal a significant correlation, which indicates that the frequency of attacks is not density-dependent, this being different to the results of other studies (Krebs and Barnard 1980; Lekuona 1999; Lekuona and Campos 2001). This could be because more cormorants did not result in a higher density, as they used a larger area when more are present, maintaining a constant bird density.

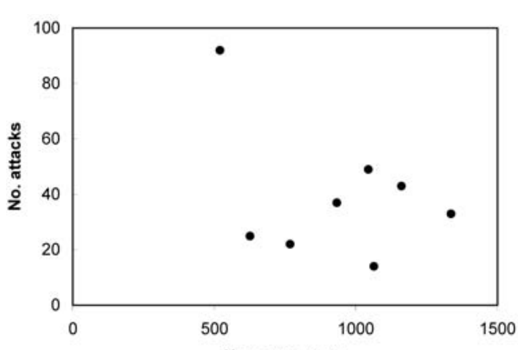

Figure 2. Relationship between the number of attacks and the total number of Great Cormorants during the study period.

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