Seasonal Patterns of Aggressiveness in Colonial Great Crested Grebes Podiceps cristatus

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Seasonal patterns of aggressiveness in colonial Great Crested Grebes *Podiceps cristatus*

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In birds, coloniality is considered to be evolutionary more advanced than solitary breeding. Territorial Great Crested Grebes *Podiceps cristatus* may engage in opportunistic colonial breeding. The present study focuses on behavioural aspects associated with clumped nesting. Based on the assumption that different agonistic interactions may trigger different costs, aggressiveness during colony establishment and subsequent nesting in the Great Crested Grebe was measured. Upon platform initiation, focal pairs claimed a territory by performing intense platform courtship. With agonistic behaviour they tried to prevent additional conspecifics from settling in their direct vicinity. As a consequence, early levels of aggression in the entire colony increased with the numbers of settled pairs. Quite quickly however, aggressiveness declined despite additional pairs settling and long before the maximum number of platforms for a particular year was reached. Two main phenomena may have contributed to the decline in aggression. First, colonial Great Crested Grebes could have been conducting behaviour consistent with the 'dear-enemy-effect'. Second, habituation to or accommodation with new neighbours could have been helped by behavioural adaptations. Focal pairs provided evidence for a relationship between aggression and egg-laying. The aggressive behaviour that was observed after clutch initiation could have been an effort to reduce the risk of intraspecific brood parasitism. Thereafter, fighting was uncommon and aggression was greatly limited to ritualized threatening. Aggression levels were higher in areas of high nesting density prior to and during egg-laying, but no longer so after clutch completion. It is concluded that colony establishment in the Great Crested Grebe is not an index of the species' sociability, but rather expresses its phenotypic plasticity to adapt to close neighbours and to contain its aggressiveness.

Key words: *Podiceps cristatus*, colonial breeding, aggressiveness, costly aggression, change in behaviour, habituation, pre-egg laying, egg laying, clutch completion

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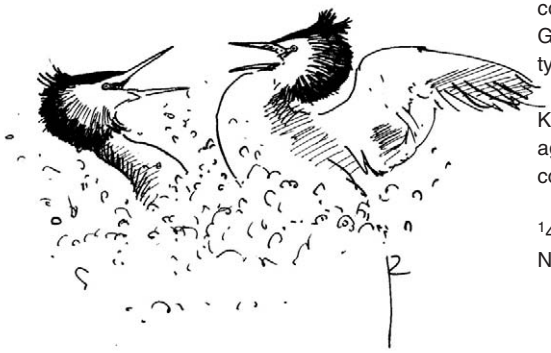

Most species of birds either breed as isolated pairs or in colonial groupings. In solitary breeders, territorial behaviour serves to space birds out through the available habitat and to exclude surplus individuals once the habitat is saturated. First arrivals establish large territories which they might later contract to some extent under pressure from later settlers (Newton 1998). Coloniality is considered to be evolutionary more advanced and the development from simply more clumped nesting to obligate colonial breeding occurs through different stages also relating to the degree of social interactions (Siegel-Causey & Kharitonov 1990). Although there are no generally accepted criteria to define the precise starting point of a colony, a definition is generally based on short average distances between nesting birds and highly synchronous breeding (Brooke & Birkhead 1991). Causal factors for colony formation may differ among unrelated groups of birds, and behavioural adaptations to change from essentially independent individuals to members of a breeding colony can represent a significant change in sociality (Siegel-Causey & Kharitonov 1990). In addition, occasions for

intraspecific brood parasitism and extra-pair copulation may increase with a more aggregated type of nesting.

The Great Crested Grebe *Podiceps cristatus* is considered as a highly aggressive solitary breeder, fiercely defending its territory, but also found to form more or less extensive colonies in most parts of its range. Different studies suggest that aggregated nesting is a phenomenon forced upon the species by the scarcity of nesting sites in relation to the superabundance of other resources (Blinov *et al.* 1981, Konter 2005, 2008a, 2008b, Vlug 1983) and nesting synchrony in colonial Great Crested Grebes is rather poor or even nonexistent (Konter 2005, 2008a, 2008b, Perry 2000, Ulenaers & Dhondt 1991). The arrival and settlement of the members of an aggregation may thus spread over a prolonged period of time. Moreover, the Great Crested Grebe could prefer breeding in isolation as the example of the Selenga River Delta showed: there, low water levels promoted colonial breeding in one year, but the rise in water levels in the next breeding season provoked a return to territorial breeding (Podkovyrov 1986).

In contrast to obligate colonial species, the building-up of nesting aggregations in the Great Crested Grebe does not spread out from a central point. On the contrary, as we could expect from solitary species, first arrivals tend to use the entire habitat available and to defend large territories (Konter 2005, 2008a, 2008b, Koshelev & Chernichko 1985). As new arrivals settle in between, the initially long distances between the grebes' platforms shrink up to 30 cm between two nests (Konter 2005). Due to the possible preference of Great Crested Grebes for solitary breeding, one could expect a continued increase in aggressiveness with increasing numbers of settled pairs and reduced distances to neighbour platforms. However, aggregated nesting seems only possible if the species has behavioural flexibility in its nesting strategy.

The present paper focuses on behavioural aspects in the nesting of opportunistic colonial Great Crested Grebes. Maintaining high levels of aggression throughout the breeding season is time and energy consuming and long-lasting intraspecific disputes entail a risk of injury. In the course of the breeding season, settled grebes are therefore expected to reduce their aggressiveness. Established pairs could react aggressively to intruders in search of a nesting space. Once new settlers have gained access to the colony, a process of habituation could then help to limit agonistic interactions between neighbours. Aggression could be more important in areas of the colony experiencing the highest intruder pressure. Especially if the pressure persists, habituation to established neighbours under whatever form may not be enough to lower the levels of aggression sufficiently. With clutch initiation, preventing damage to the eggs may gain priority over conflicting aggressive impulses in settled pairs. Therefore, a change in aggression is predicted to occur with the laying of the first egg. Based on ethological data collected on the Dutch IJsselmeer over a span of four years during colony establishment, this study provides different measurements for the development of agonistic behaviour in colonial Great Crested Grebes and discusses factors that could have influenced their social interactions.

METHODS

Study area

Data on the nesting progress, platform courtship and aggressive behaviour of Great Crested Grebes were collected at the Compagnieshaven of Enkhuizen, a yachting harbour located in the western part of the Lake IJssel (The Netherlands), from mid-March to mid-May in the years 2003–06. Lake IJssel covers approximately 122,500 ha.

The yachting harbour (52°42'N, 5°18'W) covers 14 ha, and hosted three groups of nesting pairs that qualified as colonies in the sense of Goc (1986), who arbitrarily set the upper limit of the average distance between nest platforms in a Great Crested Grebe colony to 10 m. Research activities were conducted on the Footbridge colony. The focal study area was a narrow stretch of vegetation that was easily viewed from an adjacent elevated footbridge. Settlement continued through the entire observation period with on average a maximum number of 115 platforms (range 111–122) in early May.

Field methods

In each year and for each observation period spreading generally over the weekend from Friday 10 am to Sunday 2 pm (6–10 weekends per year except in 2004 when only 4 weekends were used and no field work occurred between 2 and 25 April), all platforms found were plotted on a 1:100 map of the area. The chronology of each platform and the progress in nesting was noted. For a complete description of the area, the methods and the settlement and nesting progress, see Konter 2005, 2007, 2008a, b.

Behaviour was recorded in three different ways. The first two methods were based on all occurrences sampling (Martin & Bateson 1993 in Blumstein &

Daniel 2007) measuring aggression for the colony as a whole; the third was based on focal observations of individual pairs (Martin & Bateson 1993 in Blumstein & Daniel 2007).

(1) Fighting. On each observation day, all fights between grebes within the colony were counted and expressed as an average number of fights per hour per weekend or rate of fights F. This absolute rate of fights was divided by the number of existing platforms to obtain the relative rate of fights F/n. Fighting was assumed to involve a settled pair if the grebes were directly associated with an existing platform, and to involve intruders if the birds did not yet defend a platform. If a pair defended a platform that had not existed on the preceding observation weekend, they were considered as new settlers.

(2) Patterns of aggressiveness. In 2003, the numbers of aggressive interactions were recorded in a subsection of the colony during a minimum of eight time periods of 15 min each per observation weekend. Aggression between the grebes was classified into three categories.

Category 1: intense threatening, threat chasing (a threatening grebe swims slowly and for a distance of 1–2 m in the direction of one or two other grebes which thereupon change their direction), low threatening in the forward-display (Simmons 1965) provoking a reaction by the rival, prolonged facing while threatening.
Category 2: token diving (during low threatening, gradual disappearance into the water with surfacing in place, Fjeldså 2004), pursuit (a threatening grebe makes a fast and continued move in the direction of one or two other grebes which escape), underwater pursuit (a threatening grebe makes a fast and continued move in the direction of one or two other grebes and starts or continues the chasing with a dive).

Category 3: fighting (aggressive physical contact between two grebes) and leaving of the nest by an incubating bird to chase another grebe.

Short low intensity threats were not considered. For each observation weekend, the average number of aggressive interactions per 15 min was calculated per category and a total aggression indicator was deduced in two ways. First, by addition of average numbers in all three categories a total aggression level was obtained. The degree of ritualization of the behaviour was decreasing from category 1 to category 3, which indicated a possible increase of the risk of injury (Eibl-Eibesfeldt 1987). Therefore, as a second measure, a weighted aggression level was calculated by applying multiplication factors of 1, 2 and 3 to the average aggression in the three categories. Despite of the obvious reasons for a weighted approach, the multiplication factors chosen were arbitrary.

(3) Seasonal changes in aggressiveness. In 2005 and 2006, six individual pairs were observed for several weekends using a more detailed and comprehensive sampling protocol. Focal pairs were uniquely identified by the platforms to which they occupied. This appeared justified as from the two preceding years we had no indication that early settlers had abandoned a platform following aggressive interactions. To test for density dependence in the levels of aggression, I selected platforms located in two parts of the colony that differed in densities during previous years, the 'low-density' and 'high-density' area. If a pair associated with a particular platform disappeared early and observations were no longer possible, another nearby pair/platform was observed. Eight out of the twelve initially selected pairs were observed during the entire study period and three replacement pairs contributed data from early April onwards.

The aggressive behaviour of each pair was recorded using the categories described above. Pairs were observed for at least 30 min (on average 80 min). During each observation weekend, each platform was observed for a minimum of 6 hours over the entire daylight hours to obtain a representative sample. A total level of aggression per pair per weekend was calculated by addition of the records and division by the observation time. A weighted level of aggression was obtained by weighting the 3 categories of aggression as described above and dividing the result by the observation time. Observations of each individual were averaged by their breeding status: pre-egg-laying (PEL), egg-laying (EL) and after clutch completion (ACC).

In addition to aggressive interactions, in 2005 the following values of platform courtship of focal pairs were recorded: time used for platform courtship (seconds used for inviting, rearing, mounting, reverse mounting and post-copulation displays), number of copulation attempts (sequences of inviting, irrespective of whether mounting occurred; a sequence ended with the inviting grebe either leaving the platform or ceasing inviting and rearing for more than two minutes), number of successful copulation attempts (number of inviting sequences followed by mounting or reverse mounting). All values are expressed per observation hour.

In order to calculate how much of the aggression was related to the simultaneous presence of both mates, I differentiated between aggression displayed while one or two partners were present. To cope with

possible differences in quality among individuals (related to age, migratory profile or breeding experience), nesting parameters were assessed against the average values of the parameters for the colony as a whole.

Statistical analysis

The Kruskal–Wallis test was applied to test the significance of seasonal differences in fighting. The Mann–Whitney test served to compare density dependent aggression and platform courtship of focal pairs. The Wilcoxon Signed-Ranks test served to evaluate differences related to their breeding status. Correlation coefficients and corresponding two-tailed *t*-tests between the levels of aggression and different breeding parameters of focal pairs (numbers of platforms within a distance of 3 m (Konter 2005), differences in this number from one observation period to the next and nest content) were calculated. All statistical tests and calculations were performed using the VassarStats web site for statistical computation (http://faculty.vassar.edu/lowry/VassarStats.html).

RESULTS

Fighting

In each year, fighting occurred from late March onwards. The relative rate of fights F/n (number of fights/number of platforms) declined noticeably in early April (Fig. 1; $H = 13.58$, $df = 3$, $P < 0.005$). The yearly maximum absolute rate of fights was reached 3–4 weeks prior to the mean first egg dates for the colony (22 April 2003, 21 April 2004, 14 April 2005, 19 April 2006, Konter 2008a). This means that the rate of fights declined in spite of still increasing numbers of settled pairs.

For 102 fights from March to late April, the parties involved were identified. They involved either settled grebes and intruders in search of a nesting space (58% of all occurrences) or they occurred in the context of very recent neighbourhoods (38%). Twice in mid-April, two apparently unsettled pairs clashed on the open water surface, and in late April, two fights between two settled pairs were recorded.

Patterns of aggressiveness

The average total level of aggression displayed an increase from early April to mid-April to drop just prior to the mean clutch initiation date (22 April) for the colony. In contrast, the total number of platforms continued to increase until well into May (Fig. 2). With eggs hatching in May, the number of occupied platforms declined quickly. The levels of aggression decreased further to below those of March (Fig. 2).

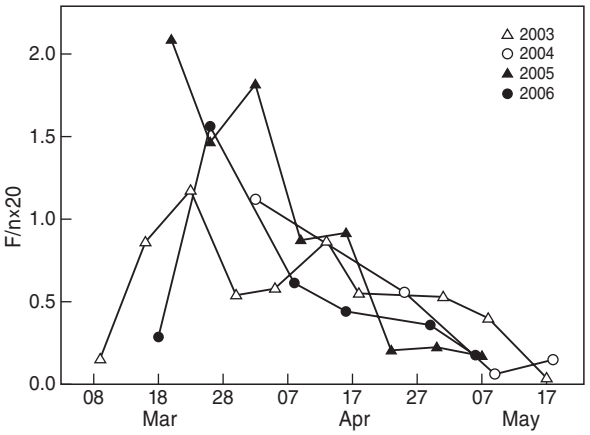

Figure 1. Seasonal pattern in the rate of fights expressed per 20 platforms, (F/n)×20, in 2003, 2004, 2005 and 2006.

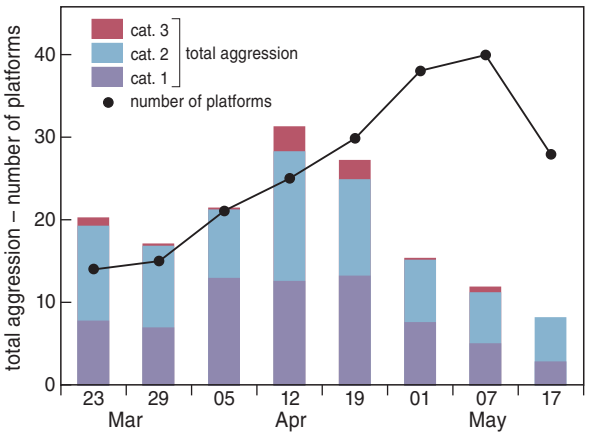

Figure 2. Seasonal pattern of total aggression with subdivision into the three categories (category 1 comprising simple ritualized threats, category 2 intense ritualized threats and pursuits, and category 3 fighting), and numbers of platforms in 2003.

Seasonal changes in aggressiveness

Though the initial values of aggressiveness were different among focal pairs, in most cases a decrease in weighted and total aggression appeared from one stage to the next. The comparison of pooled data of all focal pairs revealed decreases from one nesting stage to the next (Table 1), in particular from the egg-laying stage to the after-clutch-completion stage.

The nesting densities were 7–8 nests per 100 m^2 in the low-density area and 14–15 nests per 100 m^2 in the

high-density area. Independently of their breeding status, focal pairs in the areas with higher nesting density had higher aggression levels. Means of the weighted and total aggression were different prior to and during egg-laying (Table 1), but no longer after clutch completion.

In 2006, during pre-egg-laying costly aggression occurred irrespective of whether one or both individuals in a pair were present (46.1% against 53.9%, n = 115). After clutch completion, more costly aggression was seldom used (n = 41) and only occurred when both individuals in a pair were present.

In 2005, platform courtship of focal pairs occurred mainly during platform initiation. It dropped markedly with clutch initiation and ceased with clutch completion (Table 2). The time spent in courtship and the number of copulation attempts were significantly higher in pairs in the high-density area (z = 3.13 and z = 3.22, respectively; $P < 0.01$).

Table 1. Average levels of aggression of pairs during successive periods of the breeding cycle, in low- and high-density areas. The periods were the pre-egg-laying (PEL), egg-laying (EL) and after clutch completion (ACC) stages. Given are dates of platform initiation (PI, date in March), periods of clutch initiation (CI, days from platform to clutch initiation), and full clutch sizes (CS). All observations are from 2005 and 2006. Parameters for the low-density and high-density areas within each period are compared by Mann–Whitney tests (MW). Aggression between successive periods are compared by Wilcoxon Signed-Rank test (* = $P < 0.01$).

	Weighted aggression			Total aggression			PI days	CI days	CS
	PEL	EL	ACC	PEL	EL	ACC			
Low-density area									
Average	5.56	4.56	3.16	4.30	3.34	2.49	21.6	17.8	4.8
SE	1.69	0.38	0.57	1.42	0.25	0.42	1.5	2.6	0.73
Difference		–18% ns	–31% ns		–22% ns	–25% ns			
High-density area									
Average	16.08	12.43	5.14	12.82	9.18	4.77	21.8	17.8	4.7
SE	1.84	1.10	0.75	1.72	0.68	0.81	1.8	2.6	0.33
Difference		–23% ns	–59%*		–28% ns	–48%*			
MW z	2.64	2.65	0.82	2.64	2.65	1.37			
P	<0.005	<0.005	ns	<0.005	<0.005	ns			

Table 2. Platform courtship of focal pairs in 2005 for low- and high-density areas. Values are per observation hour. Stage: PI = platform initiation, CI = clutch initiation, CC = clutch completion.

Date	Stage	Platform courtship (sec)		Copulation attempts (n)		Successful attempts (%)	
		Mean	SD	Mean	SD	Mean	SD
Low-density area							
19.03	PI	56	37.8	0.98	0.5	92	11.8
26.03	PI	123	85.8	1.05	0.6	35	25.4
02.04	PI	105	16.0	1.27	0.1	60	2.5
09.04	CI	0	0.0	0.00	0.0	-	
16.04	CC	13	13.0	0.20	0.2	100	0.0
High-density area							
19.03	PI	435	130.4	4.28	1.2	53	6.3
26.03	PI	240	61.2	2.38	0.6	55	17.2
02.04	PI	258	46.7	2.15	0.3	43	22.1
09.04	CI	38	18.8	0.57	0.3	72	20.8
16.04	CC	9	9.0	0.14	0.1	50	0.0

DISCUSSION

Colonial nesting in the Great Crested Grebe is a forced reaction to limitations in suitable nesting habitat preventing the birds from breeding solitarily (Koshelev 1977, Podkovyrov 1986, Konter 2005). Upon platform initiation, focal pairs in this study spent considerable time performing platform courtship. Besides visibly claiming the territory, their ritual displays may simultaneously have signalled to others their readiness for defending it. Also from the start of the settling, established colonial grebes tended to prevent other pairs from settling in their vicinity and used agonistic behaviour to defend extended areas surrounding their nesting platforms. As a consequence, early in the season the levels of aggression within the colony rose together with the numbers of pairs settling. From early April onwards, a continued decline in the relative rate of fights occurred and the absolute rate of fights reached its maximum prior to the mean first egg date for the colony. It declined long before the maximum number of platforms for a particular year was reached. The pattern was confirmed by the development of aggression, except that the relative level of aggression experienced a temporarily limited increase, a priori mainly triggered by more costly aggression, around the mean date of the first egg. All focal pairs exhibited a continued decrease in aggression between successive stages of the breeding cycle, and more costly aggression disappeared after clutch completion altogether.

Without a change in the birds' agonistic behaviour, seasonal decreases in aggression could not have occurred. Fights commonly opposed well-established pairs to new settlers, and as fighting between two long-term neighbours appeared exceptional (only 2 observations in 102 fights), one may conclude that settled grebes learned to accept to some extent the presence of their neighbours and that they were capable of reducing their responsiveness towards them. This might possibly also have been a consequence of early unsuccessful disputes. Males could possibly better assess their territory after repeated interactions that may have led to conditional retaliation dependent upon the aggressiveness displayed by neighbours. This is in line with Fisher's (1954, Temeles 1994) 'dear-enemy-effect' that predicts reduced aggression towards known territorial neighbours in comparison to birds without a territory. Besides the mutual benefits from a reduction in time and energy spent in aggression, an additional profit for the neighbours could stem from defending a shared territorial boundary. The pattern is also in accordance with the low numbers of fights and low levels of aggression in late April and in May when new settlers were rare.

Habituation to or accommodation with established neighbours was possibly helped by behavioural adaptations preventing agonistic behaviour towards close neighbours. Incubating grebes typically faced in a direction so as to avoid direct eye contact with others sitting on the nest in their vicinity. Circumstantial evidence showed that grebes with a platform in the front row of the vegetated area generally approached their own nest keeping some distance from incubating close neighbours. Those with a platform further back either hurriedly passed with sleeked head feathers, lying deep in the water, or often dove to reach it. The latter was especially the case in wider and densely populated parts of the reeds. For the African Crested Grebe *P. c. infuscatus*, Dean (1977) showed that birds nesting in the centre of a colony crossed adjacent territories underwater. Also, incubating birds typically faced in a direction so as to avoid direct eye contact with others sitting on the eggs in their vicinity.

A marked change in the levels of fighting and aggression appeared each year around the mean first-egg date. High pre-egg-laying levels of aggression were followed by a reduction during egg-laying. This seemed to confirm that aggression in settled colonial Great Crested Grebes decreases with clutch initiation, which would in addition allow new pairs to intrude more easily into the colony (Koshelev & Chernichko 1985). However, during laying rather high levels of more costly aggression occurred in focal pairs, even in the absence of one mate. Also decreases in aggressiveness were more apparent after clutch completion. While it could be expected that in the interest of clutch protection agonistic behaviour dropped with clutch initiation, the avoidance of intraspecific brood parasitism (IBP) may have delayed the decreases. Species that nest in colonies experience greater IBP than those with dispersed nests (Rohwer & Freeman 1989) and its occurrence is widespread in water birds (Geffen & Yom-Tov 2001, Lyon & Eadie 2008). As shown by Koshelev and Chernichko (1985), high nesting densities in Great Crested Grebe colonies may trigger sharp increases in intra-species aggression: grebes then leave their nests, their clutches remain unobserved and provide opportunities for parasitic egg dumping. Weather hazards destroying some of the platforms in a colony may increase the risk of IBP. In Enkhuizen, only a few platforms survived a stormy night from 8 to 9 April 2005 which possibly left numerous females with egg-binding and probably put increased pressure of brood-parasitism on the few surviving platforms (Konter 2007).

Nest destruction during laying has also been identified by Henriksen (1996) as a major factor increasing parasitic egg dumping on surviving Great Crested Grebe nests.

Generally, parasitic females should have a clear interest in dumping their eggs at an early stage of the host's egg-laying, especially in species with asynchronous hatching. The order of hatching impacts the ability of offspring to compete for potentially insufficient food deliveries and, thereby, the chances of survival in a brood (Lyon 1998, Mock & Parker 1997, Moser 1986). This also holds true for grebes (Forbes & Ankney 1987, Nuechterlein 1981, Simmons 1974, 1997). In addition, eggs dumped after the host's clutch completion are very likely to be abandoned before they hatch (pers. observations for Great Crested and North American Eared Grebes *P. nigricollis californicus*). During the extended laying periods of Great Crested Grebes, the selection pressure for effective defence against brood parasitism should be intense (Rohwer & Freeman 1989). Therefore, nest defence is essential during egg-laying when the risk of brood parasitism is highest and this risk may be constrained by antagonistic interactions between hosts and parasites (Lyon 2003, Lyon & Eadie 2008).

As expected, this study provided evidence for density dependent early levels of aggression. Similarly, initial platform courtship was particularly intense in focal pairs established in areas reaching a higher final nesting density. Assuming that with each new neighbour the owner of an existing platform has to go through a process of habituation before its aggressiveness may be reduced, it seems obvious that a pair's level of aggression will be related to the final number of platforms near to it. Final nesting density could therefore be considered as a measure of the settlement pressure exerted on a particular area. As aggression was greatly reduced with clutch completion, new pairs settling close to firmly incubating birds may have been confronted with less vigorous reactions. This could also explain why focal pairs retained no significant differences in their levels of aggression after clutch completion.

In conclusion, colony establishment in the Great Crested Grebe is not an index of the species' sociability. It rather expresses the ability of the species to undergo a process of habituation allowing it to switch from a more solitary type of nesting to breeding aggregations if the ecological conditions force it to do so (Koshelev & Chernichko 1985). In general, individual levels of aggressiveness undergo a marked seasonal decrease that could be helped by behavioural adaptations towards close neighbours. The levels of aggression during egg-laying could be related to the avoidance of parasitic egg reception and this risk could partially depend on nesting density, but also on weather or other hazards. After clutch completion, clutch protection seems to be guaranteed best by the avoidance of aggression.

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SAMENVATTING

Evolutionair gezien wordt kolonievorming bij vogels als een verder ontwikkeld gedragpatroon gezien dan solitair broeden. De Fuut *Podiceps cristatus* is een territoriale soort, die echter ook kolonies kan vormen. In de onderhavige studie is het gedrag onderzocht bij Futen die in kolonies broeden. Omdat het voor de hand ligt dat agressieve interacties kosten met zich meebrengen, is het agressieve gedrag zowel gedurende de kolonievorming als het daaropvolgende broedproces gevolgd. Vanaf het moment dat Futen een platvorm om te broeden bezetten, eisten deze paren een territorium op door op dit platvorm baltsgedrag te laten zien. Soortgenoten werden vervolgens door agressief gedrag op afstand gehouden. De hoeveelheid agressie in de kolonie nam toe naarmate het aantal paren dat zich had gevestigd, toenam. Het agressieniveau van individuele paren nam echter na het innemen van een territorium sterk af, ondanks het feit dat zich nieuwe paren bleven vestigen en de kolonie zijn maximale grootte nog niet had bereikt. Twee processen hebben mogelijk bijgedragen aan deze afname in agressie. Ten eerste kunnen de vogels gehandeld hebben volgens het principe van 'dear enemies', waarbij buren elkaar niet agressief benaderen. Ten tweede kan er gewenning zijn opgetreden aan de vestiging van nieuwe buren. Tijdens de periode dat de eieren werden gelegd, nam de agressie weer toe. Misschien om tijdens deze periode broedparasitisme door soortgenoten te voorkomen. Daarna nam de hoeveelheid agressie weer sterk af. Het bleef in die periode beperkt tot geritualiseerd dreigen. In kolonies met een hoge nestdichtheid werd direct voor en tijdens de periode dat de eieren werden gelegd, meer agressie vastgesteld dan in kolonies met een lage nestdichtheid. Daarna was er geen verschil meer tussen beide kolonietypes. De auteur concludeert dat de vorming van kolonies bij de Fuut niet optreedt omdat ze sociaal zijn. Er is eerder sprake van aanpassing van het gedrag wanneer er kolonievorming optreedt, waarbij de vogels de in de loop van het seizoen fluctuerende agressie zoveel mogelijk binnen de perken trachten te houden. (KvO)

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