Etología, 3:11-22 (1993)

Colonial and solitary nesting choice as alternative reproductive tactics in birds

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ABSTRACT. *Colonial and solitary nesting choice as alternative reproductive tactics in birds.*- Some birds species have both colonial and solitary breeding behaviour. One such species is the tree sparrow *Passer montanus*, which is suitable for studying the adaptive significance of coloniality and the reasons why alternative breeding tactics can be maintained as a viable strategy. We simulated both colonial and solitary breeding situations with dense and sparce spacings of artificial nestboxes and focused on the breeding performance nesting situations. Seasonal and lifetime trend in preferring solitary breeding was found. The majority of breeding pairs chose colonial nesting in first broods, and as a higher rate of colonial than solitary breeders changed nesting situation between broods, the majority of breeding pairs nested solitarily in third broods. Females, whose reproductive performance was low shifted nesting situation between subsequent broods. Colonial pairs benefited by changing, solitary pairs benefited by retention of nesting situation in subsequent broods. Both colonial and solitary females of low productivity shifted nesting situation between subsequent breeding years. Colonial females benefited by between year changing because their productivity was higher in solitary nests than females, which retained colonial nesting. Conversely, solitary females benefited by retention of nesting situation. The majority of females bred in solitary nests in the second and third years of their return. It is possible for birds to choose different sociality on the basis of breeding experience and to attempt to improve their performance by changing nesting situation. A simple model is constructed for colonial and solitary nest choice of young and old females.

KEY WORDS. Colonial and solitary breeding, Optimal nest choice, Seasonal and lifetime trends, Tree sparrow

Some hypotheses explaining why avian coloniality evolves

Causes and consequences of living in groups have recently received much attention, both in general studies of social behaviour and in studies of social behaviour of birds. A variety of hypotheses have been adduced to explain why avian coloniality evolves, but to date the evidence available for testing those hypotheses is a best incomplete.

A common approach to evolutionary questions is to catalog first all of the likely benefits and cost experienced by individuals choosing a particular behavioural option. A few authors suggested, that a shortage of suitable nesting sites has led to the evolution of colonial breeding in birds (Lack, 1968; Snapp, 1976), but this suggestion is generally not confirmed. However, fighting for better nest material from neighbours is adventageous for the thieves and it is disadventageous for the original nest builders.

Living in a group increases the chance of finding a mate but also increases competitive interactions among the members of the colony. In many colonial species frequent extra-pair copulations have been observed, but the benefits and costs ot those extra-pair matings were different depending on the age of the individuals involved (Moller, 1987).

Crook (1962) and Lack (1968) were the first to fully recognize the adaptive significance of social foraging. Horn (1968) constructed a model -the so-called geometrical model-, which states that if food availability varies both spatially and temporarily, average flight distances are shorter for individuals breeding colonially at the center of a food distribution, rather than uniformly dispersed across the food distribution.

The information center hypothesis of Ward and Zahavi (1973) argues that species that benefit from local enhancement should also be able to benefit by following others from a central colony site. Nevertheless not all authors have been able to confirm this hypothesis.

While some colony members obtain a net benefit from kleptoparasitism, the others lost not only the food, but also suffer the cost of trying to prevent the theft. Members of colonies which benefit by brood parasitism inflict considerable costs on those members which suffer the parasitism. Egg destruction and chick killing represent a potentially severe cost of coloniality. Where cannibalism occurs, the killer of course benefits from these activities. Meanwhile desease and ectoparasites are most easily transmitted between individuals who are in close contact, and they represent other cost of life in colonies.

Some authors suggested that coloniality is an antipredator adaptation (Kruuk, 1964; Wiklund & Andersson, 1980) but several others refuted this hypothesis (Snapp, 1976; Vessem & Draulans, 1986).

In order to explain colonial behaviour it is necessary to consider each positive and negative component and it may be presumed that coloniality will evolve when the benefits from all variables exceed the costs derived from all the variables.

Some bird species have both colonial and solitary breeding behaviour. These species are therefore suitable for studying the adaptive significance of coloniality and the reasons why alternative breeding tactics can be maintained as a viable strategy. One such species is the tree sparrow (*Passer montanus* L.).

We predicted that the productivity of the parents of tree sparrow, the rate of recruiting offspring and the returning rate of adults reflect the adventage or disadventage of colonial and solitary breeding. Hence we simulated both breeding situations with dense and sparce spacings of artificial nestboxes and focused on the breeding performace of parents favouring dense or sparse nesting situations.

Five study plots were chosen in a suburban park of Budapest and 50 nestboxes were distributed in each of the study plots, 25 3-5 m apart to simulate colonial breeding and 25 sited 50 m apart to simulate solitary breeding. The distance between

TABLE I. Rate (%) of pairs switching nesting situation within a year. In parentheses number of switching pairs.

[Proporción (%) de parejas que cambian la situación de nidificación en un año.]

		Colonial moved to solitary	Solitary moved to colonial
Between first and second brood	Double breeders	11.4 (27)	10.2 (15)
	Triple breeders	28.6 (66)	8.9 (13)
Between second and third brood		20.7 (37)	9.1 (18)

neigbouring study plots was 500 m.

The nestboxes were checked at three or four day intervals from the middle of March until the end of August during the 6 years study period. Adults were caught at their nestboxes and at winter roosts, and individually marked with different combinations of colour rings. Sexes were determined by the occurence of a cloacal protuberance or a brood patch at the time of capture during the breeding season. Tree sparrows often desert nests if they are caught and marked during nest building or incubation hence trapping was restricted to nestling period. Young were individually colour ringed during the late nestling period.

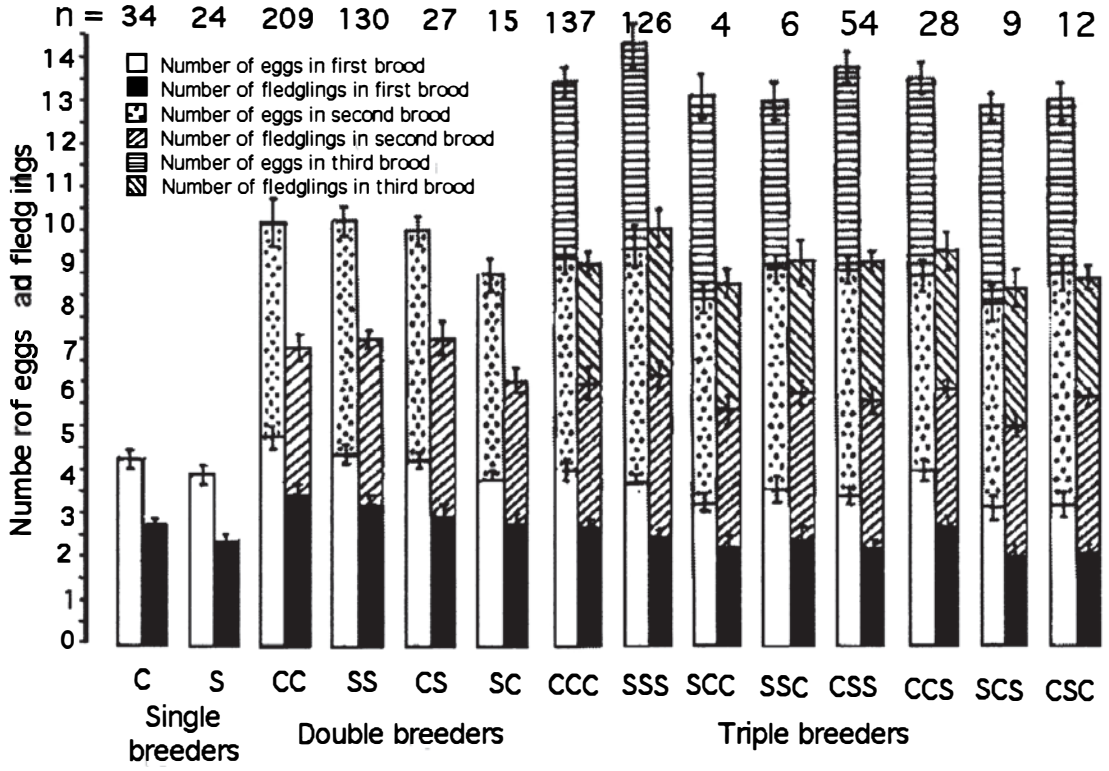

FIGURE 1. Breeding performance of tree sparrows in various nesting situations. Combined data of six study years. C and S note the broods in colonial and solitary nests. The subsequence of C and S notes first, second and third brood (For example: SCS = Solitary nesting in first brood, colonial nesting in second brood, solitary nesting in third brood). Bars note SD.

[Reproducción de *Passer montanus* en varias situaciones de nidificación.]

Seasonal and lifetime trend preferring solitary breeding in tree sparrow

Table I shows that some pairs changed nesting situation between subsequent broods. There was no difference in the rate of switching pairs between double colonial and solitary breeders (c^2=0.82, NS), but a higher rate of colonial than solitary triple

TABLE II. ANOVA for differences in breeding performances. *Pairs retained nesting situation within a breeding year. [ANOVA para las diferencias en la reproducción.]

		Breeders		Number of eggs	Number of fledglings
Between first, second and third brood		Double	F (1,379)	6.87 P=0.008	7.90 P=0.005
		Triple	F (2,373)	7.17 P=0.002	9.25 P=0.000
Between colonial and solitary pairs	First brood	Double	F (1,379)	9.13 P=0.000	9.05 P=0.000
		Triple	F (1,374)	6.74 P=0.009	7.83 P=0.005
	Second brood	Double	F (1,379)	7.95 P=0.004	8.23 P=0.002
		Triple	F (1,374)	9.82 P=0.000	4.70 P=0.029
	Third brood				
		Triple	F (1,374)	4.97 P=0.024	4.70 P=0.029
	*Total brood	Double	F (1,337)	3.44 P=0.074	2.53 P=0.193
		Triple	F (1,261)	4.80 P=0.026	6.42 P=0.012
Between colonail pairs which retained and changed nesting next brood within a breeding season	First brood	Double	F (1,234)	4.18 P=0.042	5.25 P=0.021
		Triple	F (1,229)	8.16 P=0.002	10.20 P=0.000
	Second brood				
		Triple	F (1,176)	4.28 P=0.036	5.03 P=0.023
Between solitary pairs which retained and changed nesting next brood within a breeding season	First brood	Double	F (1,143)	4.83 P=0.026	5.04 P=0.023
		Triple	F (1,143)	5.80 P=0.016	6.32 P=0.013
	Second brood				
		Triple	F (1,196)	3.94 P=0.047	4.25 P=0.038
Between pairs which retained colonial nests and moved to solitary nests	Second brood	Double	F (1,234)	8.16 P=0.000	5.28 P=0.019
		Triple	F (1,229)	9.04 P=0.000	8.84 P=0.000
	Third brood				
		Triple	F (1,176)	7.88 P=0.000	4.92 P=0.026
Between pairs which retained solitary nests and moved to colonial nests	Second brood	Double	F (1,143)	6.97 P=0.001	5.75 P=0.017
		Triple	F (1,143)	8.76 P=0.000	4.70 P=0.032
	Third brood				
		Triple	F (1,196)	6.70 P=0.004	4.28 P=0.037

breeders changed neting situation between first and second broods (c^2=20.90, p<0.001) and between second and third broods (c^2=10.06, p<0.001).

Majority of breeding pairs occupied colonial nest-boxes for first brood (62%, c^2=86.18, p<0.001). As a consequence of different shifting rate of colonial and solitary breeders there was no significant difference in proportion of pairs between colonial and solitary nesting in second brood (53% of breeders in colonies) and the proportion of colonial parents was lower (42) than that of solitary parents (c^2=13.54, p< 0.001) in third broods.

Figure 1 and ANOVA on Table II present differences in breeding performance of pairs.

1) Second broods contained most eggs and fledglings both for double and triple breeding parents, both in colonial and solitary nests. Third broods produced lower values than second but higher than first for both triple solitary and colonial breeders.

2) In first broods both double and triple breeding parents laid more eggs and reared more fledglings in colonial than solitary nests. However, the numbers of eggs and fledglings were higher in solitary than colonial nests in second and third broods.

3) Both colonial and solitary pairs changing nesting between broods laid fewer eggs and reared fewer fledglings in first broods than parents retaining nesting situation between broods; the productivity of triple breeding parents, changing between second and third broods, was lower in their second broods than that of parents which retained their nesting situation between these broods.

4) Pairs which moved to solitary nests, reared more eggs and fledglings in second and third broods than pairs which remained in colonial nests, and pairs which moved to colonial nests produced less eggs and young than pairs which retained solitary nests.

More offspring recruited per brood from colonial than solitary parents in first brood (Mann-Whitney U-test: n_1=430, n_2=265, z=4.09, p<0.001), but this

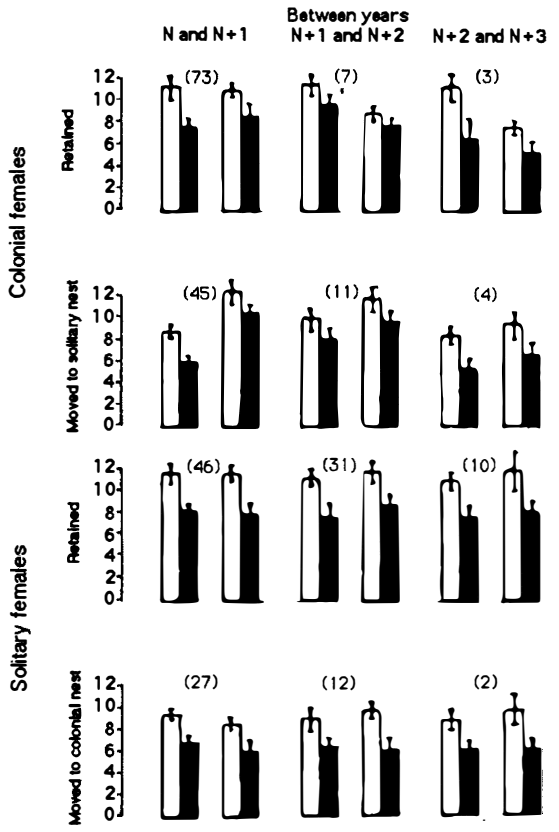

FIGURE 2. Breeding performance of females in subsequent breeding years. In parentheses number of females. Performance in years N+1 is calculated separately for females which returned between years N+1 and N+2, and performances in year N+2 is calculated separately for females which returned between years N+2 and N+3. Open column notes total number of eggs, shaded column notes total number of fledglings. Bars note SD.

[Reproducción de hembras en los años posteriores.]

relationship was reversed in second and third broods (n_1=343, n_2=302, z=2.56, p=0.010; n_1=135, n_2=180, z=2.19, p=0.028; table III). Both double and triple breeders which moved from colonial to

TABLE III. Number of recruiting young per brood in various breeding situations. In parentheses number of recruiting young.
[Número de jovenes por nidada en varias situaciones de reproducción.]

			First brood	Second brood	Third brood
Colonial nesters	All broods		0.220 (98)	0.181 (62)	0.111 (15)
	Retained in colonial nest next brood	Double breeders	0.291 (51)		
		Triple breeders	0.267 (31)	0.224 (26)	
	Moved to solitary nest next brood	Double breeders	0.120 (3)		
		Triple breeders	0.197 (13)	0.081 (3)	
Solitary nesters	All broods		0.193 (38)	0.232 (70)	0.150 (27)
	Retained in solitary nest next brood	Double breeders	0.163 (18)		
		Triple breeders	0.149 (16)	0.262 (26)	
	Moved to solitary nest next brood	Double breeders	0.143 (2)		
		Triple breeders	0.167 (2)	0.176 (3)	

solitary nests between first and second broods reared fewer recruitment young per brood than parents which retained colonial nests (U-test: n_1=25, n_2=175, z=4.26, p<0.001; n_1=66, n_2=116, z=3.84, p<0.001). Such a difference was not recorded for switching solitary breeders (U-test: n_1=14, n_2=110, z=1.70, p=0.088; n_1=12, n_2=107, z=1.38, p=0.166). Both colonial and solitary parents, which changed nesting situation between second and third broods, reared less recruiting yong per brood than parents which retained nesting situation (U-test: n_1=36, n_2=224, z=2.14, p=0.032; n_1=17, n_2=107, z=3.44, p<0.001).

Between year analysis showed that more females bred colonially than solitary in year N (61%), but this difference was not seen in year N+1 (5)5), and the relationship was reversed in years N+2 (43%) and N+3 (24%) (c^2=16.63, p<0.001; table IV). There was no difference in the rate of pairs between colonial and solitary breeders in year N according to whether they retained or changed nest spacing in year N+1 (c^2=0.52, NS); however a higher proportion of colonial than solitary pairs shifted nest spacing between years N+1 and N+2 (c^2=10.14, p<0.01). The majority of females which changed nesting within year N bred in solitary nests in N+1 (c^2=10.04, p<0.01).

We found relationships between the breeding performance and the choice by a female for either colonial or solitary nests in subsequent years (fig. 2). Productivity of colonial females which retained their nesting situation for the next year, was higher than females which moved to solitary nests (eggs and fledglings in year N: t=7.32, p<0.001 and t=5.91, p<0.001; in year N+1: t=3.05, p<0.01 and t=3.03, p<0.01; in year N+2: t=2.65, p<0.05 and

TABLE IV. Rate (%) of retention and changing of between years nesting choice of returning females. In parentheses number of returning females.
[Proporción (%) de retención y cambio de elección de nidificación, entre años, de hembras que regresan.]

		Between years		
		N and N+1	N+1 and N+2	N+2 and N+3
Colonial females	Retained	57 (73)	35 (7)	43 (3)
	Moved to solitary nest	35 (45)	55 (11)	57 (4)
	Changed nesting situation within a season next year	8 (10)	10 (2)	
Solitary females	Retained	57 (46)	72 (31)	83 (10)
	Moved to colonial nest	34 (27)	28 (12)	17 (2)
	Changed nesting situation within a season next year	9 (7)		
Females which changed nest spacing within a season	Bred in colonial nest next year	28 (8)	30 (3)	
	Bred in solitary nest next year	55 (16)	70 (7)	100 (2)
	Changed nesting situation within a season next year	15 (5)		

t=2.82, p<0.05). Performance of solitary females retaining nest spacing for the next year was also higher than for females which moved to colonies (eggs and fleglings in year N: t=8.49, p<0.001 and t=7.72, p<0.001; in year N+1: t=6.06, p<0.001 and t=5.92, p<0.001; in year N+2: t=4.16, p<0.01 and t=2.84, p<0.02).

Colonial females which moved to solitary nesting produced a higher performance than females which remained in colonies for the next year (eggs and fledglings in year n+1: t=6.10, p<0.001 and t= 9.48, p<0.001; in year N+2: t=3.65, p<0.01 and t=6.33, p<0.01; in year N+3: t=3.77, p<0.01 and t=7.36, p<0.001). Solitary females which retained nest spacing produced more eggs and fledglings in the next year than females which switched to colonies (in year N+1: t=10.18, p<0.001 and t=6.80 p<0.001; in year N+2: t=3.46, p<0.01 and t=5.43, p<0.001; in year N+3: t=5.11, p<0.001 and t=5.65, p<0.001).

Colonial females which retained nest spacing between years reared less recruiting young per brood in year N+1 and N+2 than in previous years (table V) (Mann-Whitney U-test between years N and N+1: n_1=173, n_2=181, z=3.67, p<0.001; between years N+1 and N+2: n_1=19, n_2=17, z=2.12, p=0.034). Against this, solitary females which retained nest spacing, reared more recruiting young per brood in years N+1 and N+2 than in previous years (U-test between years N and N+1: n_1=112, n_2=119, z=2.06, p=0.039; betwenn years N+1 and N+2: n_1=78, n_2=76, z=2.32, p=0.020). Colonial

TABLE V. Number of recruiting young per brood reared by returning females. Data of subsequent years of returning females are presented, so recruiting young in year N+1 are calculated separately for females which returned in N+2. Females which returned between years N+2 and N+3 did not rear recruiting young in year N+2. In parentheses number of recruiting young.

[Número de jóvenes por nidada criados por hembras que regresan.]

		Years					
		N	N+1	N+1	N+2	N+2	N+3
Colonial females	Retained in colonial nests next year	0.191 (33)	0.044 (8)	0.105 (2)	0.059 (1)		0.143 (1)
	Moved to solitary nests next year	0.098 (10)	0.101 (12)	0.125 (3)	0.200 (6)		0.090 (1)
	Changed nesting situation within a season next year	0.185 (5)					
Solitary females	Retained in solitary nests next year	0.071 (8)	0.118 (14)	0.077 (6)	0.131 (10)		0.115 (3)
	Moved to colonial nests next year	0.077 (5)	0.029 (2)		0.074 (2)		
Females changed nest spacing within a year	Moved to solitary nests next year		0.087 (2)				

females which moved to solitary nests between years N and N+1 and between years N+1 and N+2 raised more recruiting young both in years N+1 and N+2 than females which retained colonial nests in subsequent years (U-test for year N+1: n_1=119, n_2=181, z=2.27, p=0.023; for year N+2: n_1=30, n_2=17, z=4.15, p<0.001). Solitary females, which moved to colonies between subsequent years reared less recruiting young in years N+1 and N+2 than females which retained solitary nest spacing (U-test for year N+1: n_1=69, n_2=119, z=3.64, p<0.001; for year N+2: n_1=27, n_2=76, z=2.77, p=0.006).

Colonial and solitary breeding may be maintained as viable reproductive strategy

It is possible for birds to choose different sociality on the basis of breeding experience and to attempt to improve their performance by changing nesting situation. Switching pairs seem to be in poorer condition before changing and as the move from colonial to solitary breeding is adventageous both by within and between years changing, the

future gains, which is predicted by the female is justified in solitary spacing. Nevertheless colonial nesting is more adventageous than solitary nesting is first broods, the majority of female retain colonial breeding through the season in their first year.

A simple model might be constructed for colonial and solitary nest choice of young and old female (fig. 3). The majority of first year female which successfully reared many fledglings with relatively low costs, did so in colonies, only a few female bred solitarily. Those first year females which suffered higher costs, bred solitarily in higher proportion, and when breeding performance was low with high costs, first year female changed their nesting situation next year.

The majority of old females benefited by breeding solitarily and increasing breeding performance with decreasing costs reflects an increasing proportion of solitary breeders in old females. As a consequence rate of colonial breeders declined steeply in subsequent years.

The final question is why alternative breeding tactics may be maintained as a viable reproductive strategy, and which species may be able to choose between colonial and solitary breeding throughout life.

There seem to be three principal factors which are likely to indicate the retention of alternative

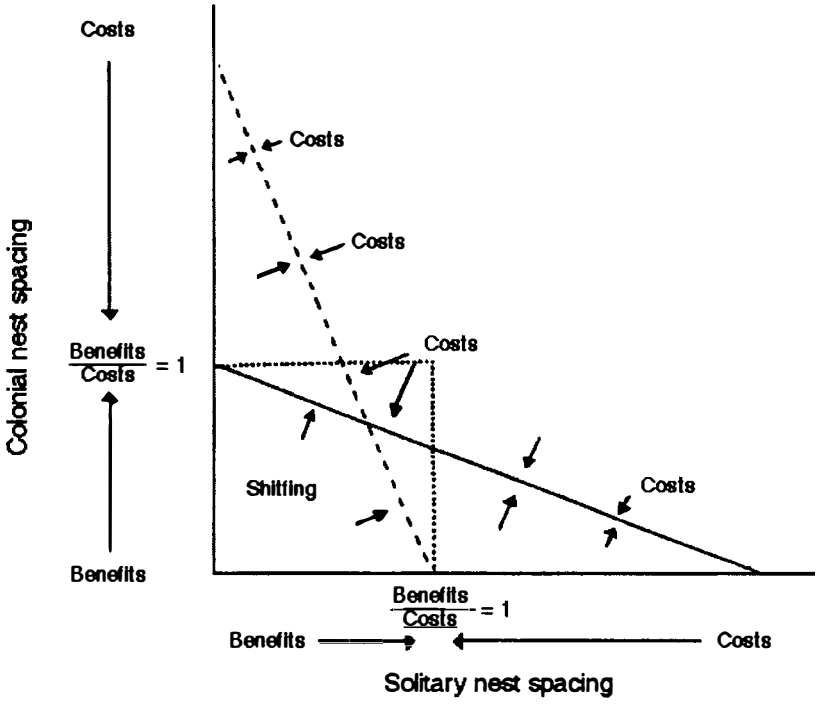

FIGURE 3. Simple model for colonial and solitary nest choice of young and old females. Dashed line notes the fragments of young breeding population, unbroken line notes the fragments of old breeding population.
[Modelo simple para la elección, por parte de hembaras viejas y jóvenes, de nido solitario y colonial.]

breeding tactics. The first is multibreeding. Species should be able to breed two or three times within a breeding season. The second is a change of food resource during the breeding season. Food environment should become richer and/or more diverse as the season progresses (there is an adaptative adjustment of tree sparrow to increased food supply: parents rear more fledglings in second and third broods than in first broods). The third factor is the difference in breeding experience between young and old female.

In first broods, colonial breeding is adventageous for young parents because they acquire experiences from companions, but by second and third broods, when they are able to collect food from a predictable food environment, solitary breeding is adventageous because they have already acquired the necessary experience and now want to avoid competition. Older parents which have adquired knowledge about the feeding and nesting environment and have successfully reared large broods in solitary spacing, prefer solitary nesting behaviour.

Summary

Shortage of suitable nesting sites, chance of finding a mate, social foraging, competition for food, kleptoparasitism, brood parasitism, egg destruction, chick killing, transmission of desease and ectoparasites, predation pressure as main effects may cause positive and/or negative responses in the colonial individuals. It may be presumed that coloniality evolves when the benefits from all variables exceed the costs derived from all the variables. Tree sparrows (*Passer montanus* L.) have both colonial and solitary breeding behaviour, therefore this species is suitable for studying the adaptive significance of coloniality and the reasons why alternative breeding tactics can be maintained as a viable strategy. We simulated both colonial and solitary breeding situations with dense and sparce spacings of artificial nestboxes and focused on the breeding performance and the returning rate of tree sparrows favouring dense or sparce nesting situations. Seasonal and lifetime trend in preferring solitary breeding was found. The majority of breeding pairs chose colonial nesting in first broods, and as a higher rate of colonial than solitary breeders changed nesting situation between broods, the majority of breeding pairs nested solitarily in third broods. Females, whose reproductive performance was low shifted nesting situation between subsequent broods. Colonial pairs benefited by changing, solitary pairs benefited by retention of nesting situation in subsequent broods. Both colonial and solitary females of low productivity shifted nesting situation between subsequent breeding years. Colonial females benefited by between year changing because their productivity was higher in solitary nests than females, which retained colonial nesting. Conversely, solitary females benefited by retention of nesting situation. The majority of females bred in solitary nests in the second and third years of their return. It is possible for birds to choose different sociality on the basis of breeding experience and to attempt to improve their performance by changing nesting situation. There seem to be three principle factors which are likely to indicate the retention of alternative breeding tactics as a viable reproductive strategy. (1) Multibreeding. Species should be able to breed two or three times within a breeding season. (2) Food environment should become richer and/or more diverse as the season progresses. (There is an adaptive adjustment of tree sparrow to increase food supply: parents rear more fledglings in second and third broods than in first broods). (3) Difference in breeding experience between young and old parents. Older parents which have acquired knowledge prefer solitary nesting behaviour.

Resumen

Elección entre nidificación colonial y solitaria como tácticas reproductivas alternativas en aves.

En los individuos coloniales como efectos principales la escasez de lugares de nidificación adecuados, la posibilidad de encontrar una pareja, la alimentación social, la competición por alimento, el kleptoparasitismo, el parasitismo de incubación, la destrucción de huevos, la muerte de pollos, la transmisión de enfermedades y de ectoparásitos y la presión de depredación pueden casusar respuestas positivas o negativas. Su puede suponer que la colonialidad se desarrolla cuando los beneficios de todas las variables sobrepasan los costos derivados de ellas. *Passer montanus* presenta comportamiento de nidificación tanto colonial como solitario, por lo que esta especie es adecuada para el estudio del significado adaptativo de la colonialidad, así como de las razones por las que las tácticas de reproducción alternativas se pueden mantener como una estrategia viable. Simulamos situaciones de nidificación, tanto coloniales como solitarias, con espaciamiento denso y no denso con cajas nido y analizamos la reproducción y la tasa de regreso de esta especie que favorecen ambas situaciones de espaciamiento. Se encontró una tendencia de reproducción solitaria tanto estacional como durante la vida. La mayoría de las parejas eligen nidificación colonial para su primera puesta y como una mayor tasa de reproductores coloniales que solitarios cambiaron la situacion de nidificación entre puestas, la mayoria de las parejas reproductoras nidificaron de forma solitaria en la tercera puesta. Las hembras cuya reproducción fue baja cambiaron la situación de nidificación entre subsecuentes puestas. Las parejas coloniales se beneficiaron por el cambio, mientras que las solitarias lo hicieron por el mantenimiento de la situación de nidificación en puestas posteriores. Las hembras de baja productividad, tanto solitarias como coloniales, cambiaron la situación de nidificación entre años. Las hembras coloniales se beneficiaron del cambio de situación de nidificación entre años ya que su productividad fue mas alta en nidos solitarios que las que conservaron la condición colonial. Por el contrario, las hembras solitarias se beneficiaron por mantener su situación de nidificación. La mayoría de las hembras nidificaron en nidos solitarios el segundo y tercer año de su regreso. Es posible para aves elegir diferente socialización sobre la base de su experiencia reproductora e intentar mejorarlas cambiando la situación de nidificación. Parece haber tres factores principales que pueden indicar la retención de tácticas de nidificación alternativa como una estrategia reproductiva viable. (1) Reproducción múltiple. Las especies deberían ser capaces de nidificar dos o tres veces en la misma estación. (2) El alimento debería llegar a ser mas rico y/o mas diverso a medida que avanza la estación (hay un ajuste adaptativo de *P. montanus* a incrementar el suplemento alimenticio: los padres crían mas volantones en las segundas y terceras puesta que en las primeras). (3) Diferencias en experiencia reproductora entre padres jóvenes y viejos. Los padres mas viejos que han tenido experiencia prefieren nidificar en solitario.

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(Recibido: agosto 1993)