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Cooperation and conflict in the building and maintenance of the compound nests of monk parakeets *Myiopsitta monachus*

F. S. E. Dawson Pell¹, J. C. Senar² , A. Ortega-Segalerva²,
B. J. Hatchwell¹ 

Author affiliations:

¹University of Sheffield, UK
²Museu de Ciències Naturals de Barcelona, Spain

Corresponding author:

Juan Carlos Senar
jcsenar@bcn.cat

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Martina Carrete

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Abstract

Cooperation and conflict in the building and maintenance of the compound nests of monk parakeets Myiopsitta monachus. Colonial birds often breed at high density, generating conflict among neighbours over the use of nest-building materials. However, in a few colonial species, breeders appear to cooperate in the construction of compound nests that contain multiple breeding chambers within a single nest structure. The relative contributions of individual birds and the balance between cooperation and conflict among close neighbours in such species have rarely been examined. In this study, we investigated evidence for cooperation and conflict in the building and maintenance of the nests of monk parakeets *Myiopsitta monachus* in an invasive population in which compound nests are frequent. First, we found that males invested more in nest construction than females and when more than one male occupied the same breeding chamber multiple males contributed to the same nest. Females, by contrast, invested more in nest defence than males. Second, we found that there was conflict among pairs over nest material, with kleptoparasitism of nesting material and defence against conspecifics evident. We conclude that nest-building in monk parakeets involves both cooperation and conflict. Breeders often tolerate the budding of nests, which are often built by relatives, but that pairs are also in conflict over the use of nest material.

Key words: Breeding behaviour, Monk parakeet, *Myiopsitta monachus*, Parrot, Kleptoparasitism, Parentage

Resumen

Cooperación y conflicto en la construcción y el mantenimiento de los nidos compuestos de la cotorra argentina, Myiopsitta monachus. Las aves coloniales suelen criar en comunidades con una alta densidad, lo que genera conflictos entre los vecinos por el uso de materiales para la construcción del nido. Sin embargo, en algunas especies coloniales, los individuos reproductores parecen cooperar en la construcción de nidos compuestos, que contienen múltiples cámaras de cría, pero mantienen una estructura de nido único. La contribución relativa de los individuos y el equilibrio entre la cooperación y el conflicto entre vecinos cercanos son aspectos muy poco estudiados en estas especies. En este estudio, analizamos los indicios de cooperación y conflicto en la construcción y el mantenimiento de los nidos de las cotorras argentinas, *Myiopsitta monachus*, en una población invasiva en la que los nidos compuestos son frecuentes. En primer lugar, observamos que los machos invirtieron más en la construcción del nido que las hembras y que cuando más de un macho ocupaba la misma cámara de cría, múltiples machos contribuían al mismo nido. En cambio, las hembras invirtieron más en la defensa del nido que los machos. En segundo lugar, constatamos que se generaban conflictos entre parejas por el material de nidificación y que se producían episodios de cleptoparasitismo de material de nidificación y de defensa en contra de ejemplares conspecíficos. Concluimos que la construcción de los nidos de las cotorras argentinas trae consigo cooperación y conflictos. Los reproductores suelen tolerar que se vayan construyendo nidos adosados al ya existente, a menudo por parientes, pero esas parejas también entran en conflicto por el uso del material de nidificación.

Palabras clave: Comportamiento reproductor, Cotorra argentina, *Myiopsitta monachus*, Cotorra, Cleptoparasitismo, Parentesco

Introduction

Many bird species aggregate to breed in colonies, often at very high densities, but each breeding pair usually has a discrete nest in which they raise their offspring (Rolland et al 1998). In a small number of cooperatively breeding birds, pairs exhibit more extreme aggregation, co-breeding or joint-nesting females laying their eggs in a communal nest, in which the offspring of multiple breeders are raised alongside each other (Riehl 2013). The social organisation of such species is variable (Vehrencamp and Quinn 2004), well-studied examples including acorn woodpeckers *Melanerpes formicivorus*, in which female co-breeders are typically related (Koenig et al 2016), while in crotophagine cuckoos (Riehl 2021) and Taiwan yuhinas *Yuhina brunneiceps* (Shen et al 2016) co-breeders are unrelated. In a handful of species, an intermediate form of aggregated breeding occurs, in which multiple pairs or breeding groups each occupy a discrete nest chamber within a larger communal structure, usually described as a compound nest (Collias and Collias 1977).

Compound nest structures are routinely recorded in just four species of birds, the social organisation and breeding system of which varies widely. The palmchat *Dulus dominicus* from Hispaniola, the only species in the family Dulidae, builds a multi-chambered compound stick nest that may be 2 m in diameter and contain 4–10 separate chambers, but with a range of 1–50. Little is known of the palmchat's breeding biology but they are thought to breed in pairs, each occupying a separate chamber but with frequent intraspecific brood parasitism (del Hoyo et al 2005). In the family Ploceidae, compound nests are built by two species. Red-billed buffalo weaver *Bubalornis niger* nests have an average of five chambers per nest, each chamber occupied by a breeding female. Compound nests are typically controlled by two unrelated males, a form of cooperative polygynandry, with both males contributing to construction of the communal structure (Winterbottom et al 2001). Another ploceid, the sociable weaver *Philetairus socius*, builds the most substantial compound nests of any bird, sometimes weighing several tonnes, housing > 100 separate nest chambers and lasting for decades. Nest chambers are embedded beneath a communal thatch that provides thermoregulatory benefits and which is not simply a product of nest chamber construction, but rather is a public good requiring communal investment (White et al 1975, Bartholomew et al 1976, van Dijk et al 2013). Unlike red-billed buffalo weavers, sociable weavers are clustered with relatives in compound nests (van Dijk et al 2015) and they exhibit kin-directed cooperative breeding with helpers typically assisting close kin in raising their offspring (Covas et al 2006). More significant in the context of nest-building is that the chambers of related males are spatially clustered within a compound nest and males invest in cooperative building of the communal thatch adjacent to their own and their relatives' chambers (van Dijk et al 2014).

The only other bird species that routinely breeds in multi-chambered compound nests is the monk parakeet, *Myiopsitta monachus* (Psittacidae). Monk

parakeets are native to South America, but they have successfully established invasive populations outside the native range across South and North America, Europe and Asia (Forshaw 1989, Russello et al 2008, Bush et al 2014). Uniquely amongst parrots, monk parakeets are not cavity-nesters; instead they use interlaced sticks to construct large, conspicuous nests that may contain a single nest chamber or multiple chambers in a compound structure (Forshaw 1989, Eberhard 1998, Spreyer and Bucher 1998). The nests vary widely in size and number of occupants; single nests have been reported to contain up to 100 pairs of parakeets (Naumburg 1930, Burger and Gochfeld 2005). However, where the species is heavily managed, such as in urban areas in their invasive range, the number of chambers per nest is typically lower. For instance in Catalonia the majority of nests contain only one or two chambers, although nests with up to 36 chambers have been reported (Domènech et al 2003). Nest structures are frequently aggregated, with groups of nests occupying the same or neighbouring trees (Bucher et al 1991, Eberhard 1998). Previous studies have revealed that relatives are clustered within these compound nests and within shared nesting trees, resulting in 'kin-neighbourhoods' that form through limited and coordinated natal dispersal and high breeding site fidelity (Dawson Pell et al 2021).

Monk parakeets are also unusual in being among the 5% of parrot species that are described as cooperative using a broad definition that includes cooperative polyandry and polygynandry (Cockburn 2006). Evidence of cooperative breeding was largely anecdotal (Bucher et al 1991, Eberhard 1998; Bucher et al 2016), but Dawson Pell (2021) showed that in an invasive population in Barcelona, approximately 20% of breeding units comprise three or more adults. Some groups comprised breeding pairs with retained offspring, but others included co-breeders that could be male or female. Genetic and pedigree evidence revealed that groups are typically, but not always, composed of kin. Moreover, relatives are spatially clustered within compound nests and within nesting trees (Dawson Pell et al 2021), suggesting that their breeding system is similar to that of sociable weavers. However, little is known of the extent of cooperation and conflict between occupiers of their unusual compound nests.

In this study, our overall aim was to use field observations to investigate the nest-building behaviour of an invasive urban population of monk parakeets, addressing two specific objectives. First, we aimed to characterise the relative contributions to nest-building and maintenance by males and females in pairs and groups. Second, we assessed the evidence for cooperation and conflict over nest-building among members of pairs and groups.

Methods

Study site and species

We observed the nest-building behaviour of monk parakeets at nests in Ciutadella Park, Barcelona, on the north-east coast of the Iberian Peninsula

(41.39°N 2.17°E). There is a high density of monk parakeet nests in Ciutadella Park, sited mainly > 5 m from the ground in pine (*Pinus* spp.) and palm (*Phoenix* spp.) trees. Monk parakeets in the park are habituated to humans and their behaviour around nests is readily observed from the ground without causing disturbance. Approximately 64% of the breeding population of monk parakeets in our study area were marked using leg rings and highly visible, unique neck collars that enable individual identification up to 40 m distance (Senar et al 2012). Birds were captured using either gas-propelled nets or a baited trap, or we caught birds in the nest during incubation, or ringed them as nestlings, using a cherry picker to access nests. Monk parakeets cannot be sexed reliably from their morphology so observations were collected blind to sex, which was determined subsequently by molecular genetic means. Blood samples (maximum 100 µl) were extracted from the brachial or jugular vein during ringing and birds were sexed using the sexing marker Z002B (Dawson 2007, Dawson Pell et al 2020). JC Senar received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07. Birds were handled and blood samples taken with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds.

Monk parakeet breeding units are either pairs (c. 80%) or groups of three to five birds (c. 20%), additional birds being either co-breeders or non-breeders of either sex that may or may not be related to other group members (Dawson Pell 2021). Breeding unit composition was determined by observing the number of individuals attending a nest chamber. If any unringed birds were present, the maximum number of unringed birds attending at the same time was recorded.

Nest-building observations

We observed nest-building at nests in ten mature pine trees, *Pinus halepensis*, in Ciutadella Park between April and July in 2018 and 2019. Each nest chamber was individually labelled with a numbered tag visible from the ground, and each nest was observed for one hour every two-seven days in 2018 and one hour every two-eleven days in 2019. Multiple nests were observed simultaneously in a single nesting tree by the observer (FSE Dawson Pell) from the ground using binoculars. Observations at each nest alternated between the morning and afternoon, and between early and late morning/afternoon so that the range of available daylight hours was covered. A total of 390 observation hours were conducted across two years (2018: 263 h, 22 h/chamber; 2019: 127 h, 14-15/chamber).

In the 10 focal pine trees there were 72 nests containing 149 individual nest chambers by the end of observations in 2018. Of these, 112 chambers were occupied and 74 were used in breeding attempts by 113 marked birds and at least 64 unmarked birds. In 2019, there were 81 nests containing 98 chambers,

92 of which were occupied and of these, 76 were used in breeding attempts. There were fewer unoccupied chambers and fewer compound nests in the 10 trees we observed in 2019 due to management activities that removed all the monk parakeet nests in pine trees in July 2018. Note that the smaller number of nests with multiple chambers may potentially have affected the levels of cooperation and conflict over nest construction (see Results). Nests in 2019 were occupied by 103 marked individuals and at least 64 unmarked individuals. The age of observed birds ranged from one year old to at least 13 years old.

During nest observations we recorded all incidents of nest-building and maintenance behaviours, theft of nesting material and nest defence. We considered the delivery of new nesting material collected away from the nest to be nest-building behaviour and we defined nest maintenance behaviours as when existing nest material was manipulated or moved around the same nest structure. For all nests included in analyses we observed both building and maintenance behaviours. Nest material kleptoparasitism was recorded when nest material was taken from one nest and delivered to another. Nest defence was defined as any occasion that an individual attempted to displace a bird that was attempting to steal nesting material from their nest, including vocalisations and/or chases. All behavioural observations were made blind to the sex of birds.

Statistical methods

To examine whether nest building behaviour differed between the sexes or between pairs and groups, we initially conducted a negative binomial GLMM on the number of building events, including individual identity as a random factor, and sex, breeding unit (group/pair), the interaction between sex and breeding unit, and year as fixed effects. However, only around half of the birds were observed in both years, so the random effect prevented model convergence. Therefore, we applied a negative binomial GLM including the data for all individuals, that included sex, breeding unit, the interaction between sex and breeding unit, and year as explanatory factors. We then ran a second analysis on a more conservative dataset that included data for birds that were observed in just one year, to rule out the possibility that any results in the first analysis were driven by repeated observations on certain individuals. We repeated the same two analyses on the number of maintenance events. Model simplification was through stepwise backwards elimination (Crawley 2005) and models were compared using likelihood ratio tests. Variables were removed by order of least significance. Significance values for retained terms were obtained by comparing the minimal model with a model from which we removed the term of interest. P-values for dropped terms were calculated by comparisons between the minimal model without the term included and a model including the term. For groups, we also examined the building and maintenance efforts of group members to determine whether they differed in their investment in the shared nest.

Table 1. Negative binomial GLM examining factors affecting the observed numbers of building and nest maintenance events by individuals: A, C, models including all individuals (N = 206 birds: 83 females, 123 males, 139 in pairs, 67 in breeding groups). B, D, individuals observed in only one year (N = 66 bird: 25 females, 41 males, 39 in pairs, 27 in breeding groups). We present information on terms in the final models and those removed. Terms were considered significant at $p < 0.05$. Dropped terms indicated in italics. Effect sizes (\pm SE) were obtained from the minimal model in each case. We individually returned terms removed during model selection to the minimal model to assess significance using likelihood ratio tests, where appropriate also including individual terms from the interaction in this assessment.

Tabla 1. Modelo lineal generalizado binomial negativo que examina los factores que afectan a las cifras observadas de episodios de construcción y mantenimiento de nidos por los individuos: A, C, modelos que incluyen a todos los individuos (N = 206 aves: 83 hembras y 123 machos, 139 en pareja y 67 en grupos de reproducción). B, D, individuos observados en solo un año (N = 66 aves: 25 hembras y 41 machos, 39 en pareja y 27 en grupos de reproducción). Presentamos información sobre los términos incluidos en los modelos finales y los términos eliminados. Los términos se consideraron significativos a $p < 0,05$. Los términos eliminados se indican en cursiva. La magnitud de los efectos (\pm SE) se obtuvo a partir del modelo mínimo en cada caso. Volvimos a incluir en el modelo mínimo cada uno de los términos eliminados durante la selección de modelos a fin de evaluar la significación utilizando el contraste de la razón de verosimilitudes y, si procedía, incluyendo también los términos correspondientes a la interacción en esta evaluación.

Model	Parameter	Estimate \pm SE	t	p
A. Nest building: all individuals	(Intercept)	0.657 \pm 0.147	4.466	< 0.001
	Sex	2.384 \pm 0.155	15.426	< 0.001
	Year	-0.742 \pm 0.137	-5.419	< 0.001
	Group member	-0.319 \pm 0.146	-2.195	0.031
	<i>Group * sex</i>			0.819
B. Nest building: individuals observed in one year only	(Intercept)	0.265 \pm 0.293	0.904	0.366
	Sex	2.376 \pm 0.317	7.504	< 0.001
	Group member	-0.647 \pm 0.274	-2.363	0.023
	Year			0.244
	<i>Group * sex</i>			0.940
C. Nest maintenance: all individuals	(Intercept)	1.315 \pm 0.115	11.428	< 0.001
	Sex	0.738 \pm 0.132	5.588	< 0.001
	Year	-1.084 \pm 0.131	-8.291	< 0.001
	<i>Group member</i>			0.366
	<i>Group * sex</i>			0.596
D. Nest maintenance: individuals observed in one year only	(Intercept)	1.049 \pm 0.238	4.404	< 0.001
	Sex	0.668 \pm 0.275	2.433	0.019
	Year	-0.688 \pm 0.275	-2.502	0.016
	<i>Group member</i>			0.800
	<i>Group * sex</i>			0.790

We ran similar models examining the number of kleptoparasitic events that occurred, including sex and year as explanatory factors. For nest defence, due to low sample sizes we ran just one model that included all individuals and sex and year as explanatory factors (excluding one nest defence event by a non-resident). All statistical analyses were performed in R version 3.5.0 (R Core Team 2018).

Results

Contributions to nest-building and maintenance

Male monk parakeets built and maintained nests significantly more often than females (table 1; fig. 1A, 1B). Birds that bred in groups were observed engaging in building work significantly less than birds in pairs (table 1A, 1B; fig. 1C), but there was no difference in the maintenance activity of birds in groups and pairs (table 1C, 1D; fig. 1D; note that higher building activity in 2018 than in 2019 reflects longer observation time in that year). To examine relative contributions of individuals to nest-building and maintenance within breeding groups, we focused on males because they contributed most to both activities (fig. 1A, 1B).

The contribution of different males varied between nests: in 11/14 multi-male groups in which building was observed (79%), all males engaged in building activity, while in the remaining three groups (21%) one male was not observed building. Similarly, in 12/13 multi-male groups in which nest maintenance was observed (92%), all males contributed at least once. These results suggest that most or all males contribute to building and maintaining nests although effort may be split unevenly among them.

We observed parakeets taking sticks (N = 2,560), palm leaves (N = 47) and grass (N = 1) to their nests as building material. Almost all items were taken to a focal bird's own nest, containing either a single chamber or part of a compound nest. Just two items were taken to another nest and on both occasions it was to a nest adjacent to their own. Nest maintenance, i.e. birds removing a stick from the nest structure and inserting it in a new position or simply manipulating a stick in the same location, was observed on 1,167 occasions and, as for building, all observations of marked birds involved maintenance behaviours at a bird's own nest. Within a compound nest, there is no clear demarcation between the structures of adjacent chambers,

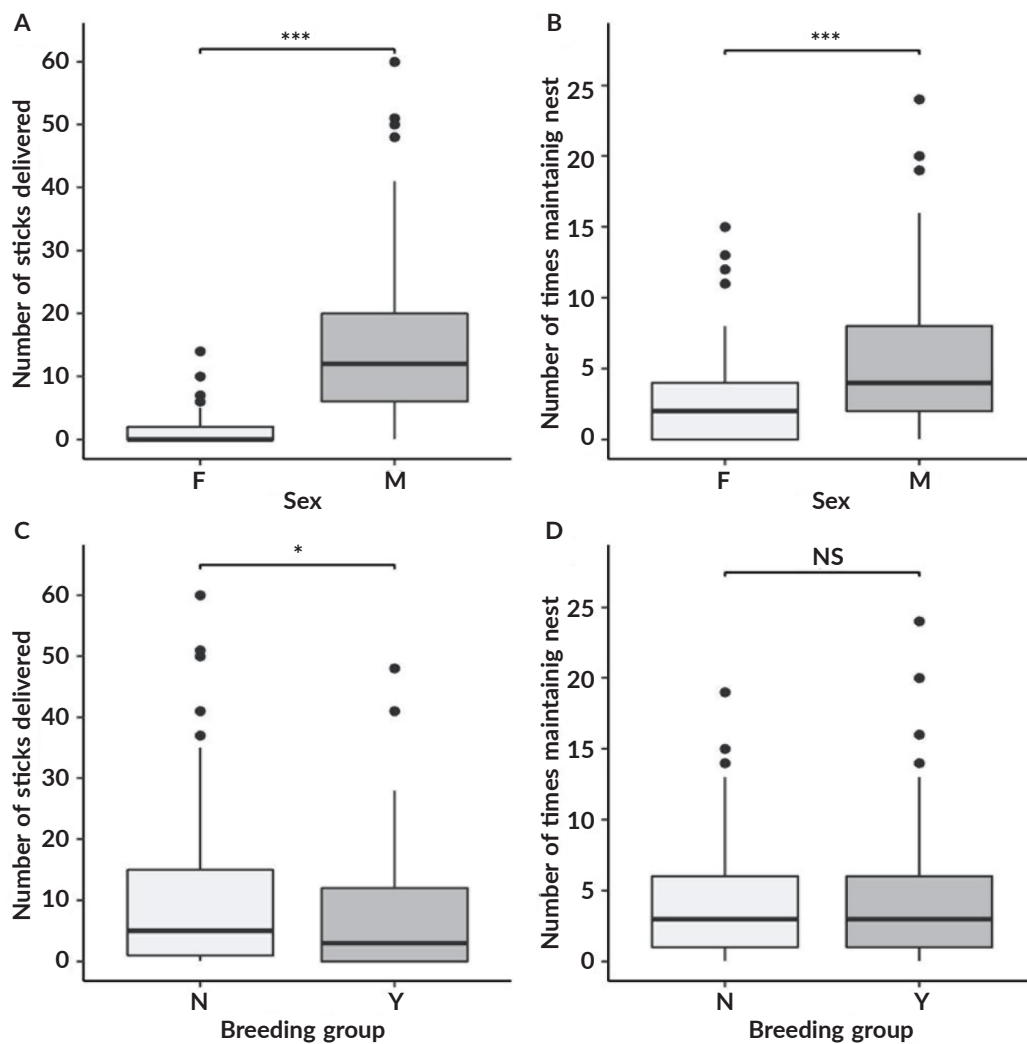


Fig. 1. Nest building (A) and maintenance behaviour (B) of female (F) and male (M) monk parakeets (N = 206 birds: 83 females, 123 males). Nest building (C) and maintenance behaviour (D) for birds in a breeding group (Y) and breeding pairs (N) (N = 206 birds: 139 in pairs, 67 in breeding groups). Data for all individuals shown for both years. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). *** $p < 0.001$, * $p < 0.05$.

Fig. 1. Comportamiento de construcción (A) y mantenimiento (B) del nido en hembras (F) y machos (M) de cotorra argentina (N = 206 aves: 83 hembras y 123 machos). Comportamiento de construcción (C) y mantenimiento (D) del nido observados en las aves de un grupo de reproducción (Y) y en parejas reproductoras (N) (N = 206 aves: 139 en pareja y 67 en grupos de reproducción). Se muestran los datos relativos a todos los individuos en ambos años. En los diagramas de caja se indica el intervalo intercuartílico (límites superior e inferior de las cajas), la mediana (líneas gruesas dentro de las cajas), los niveles máximos sin contar los valores atípicos (líneas que se extienden fuera de las cajas) y los valores atípicos (puntos). *** $p < 0,001$, * $p < 0,05$.

so building activity could not always unequivocally be assigned as directed towards a particular nest. For example, a bird may insert a twig midway between two chambers occupied by different pairs. Nevertheless, birds were never observed entering a nest chamber that was not their own to build.

Of 2,560 sticks observed being delivered, at least 567 (22%) were stolen from other nests, and a further 180 unsuccessful attempts at stick theft were also observed. Both sexes were observed stealing nest material but males did so significantly more than females (table 2A, 2B; fig. 2A). The great majority (90–98%) of recorded thefts were from nests within the tree the

thief nested in, the remainder being from nests in a neighbouring tree. However, this estimate of the frequency of theft is conservative because we assumed that sticks brought to the nest from a distance and not directly observed being collected or stolen, were collected rather than stolen.

Birds frequently defended their nests against kleptoparasites. Of 194 nest defence events recorded, 172 (89%) prevented kleptoparasitism and in just 22 (11%) cases did the kleptoparasite succeed in stealing material. In contrast to nest-building and stick theft, females defended nests significantly more than males (fig. 2B, table 2C). Defence events involved either a

Table 2. Negative binomial GLM examining factors affecting the observed numbers stick theft by individuals and the numbers of nest defence events: A, C, models including all individuals (N = 206 birds: 83 females, 123 males). B, individuals observed in only one year (N = 66 birds: 25 females, 41 males).

Tabla 2. Modelo lineal generalizado binomial negativo que examina los factores que afectan al número observado de ramas robadas por los individuos y al número de episodios de defensa del nido: A, C, modelos que incluyen a todos los individuos (N = 206 aves: 83 hembras y 123 machos). B, individuos observados en solo un año (N = 66 aves: 25 hembras y 41 machos).

Model	Parameter	Estimate ± SE	t	p
A. Kleptoparasitism: all individuals	(Intercept)	-1.010 ± 0.291	-3.473	< 0.001
	Sex	2.551 ± 0.319	7.994	< 0.001
	Year	-1.038 ± 0.270	-3.838	< 0.001
B. Kleptoparasitism: individuals observed in one year only	(Intercept)	-1.061 ± 0.538	-1.974	0.048
	Sex	2.476 ± 0.607	4.080	< 0.001
	Year	-1.366 ± 0.559	-2.445	0.014
C. Nest defence: all individuals	(Intercept)	0.396 ± 0.221	1.791	0.073
	Sex	-0.857 ± 0.277	-3.093	0.002
	Year	-1.175 ± 0.297	-3.951	< 0.001

single bird chasing the thief (N = 182), or two birds acting together (N = 12); in six cases the joint defence was confirmed to be by a pair (N = 4) or members of the same breeding group (N = 2).

Discussion

The building and maintenance of the elaborate stick nests of monk parakeets is characterised by both cooperation and conflict. Both sexes within pairs contribute to the construction of nests and their maintenance, although males invest more than females in both activities. Conversely, females invest more than males in defence of the nest against kleptoparasites. In groups, multiple males invest in nest-building, although the share of work among them is not necessarily even. In compound nests, individuals were only observed entering their own chamber to build, but in the absence of clear demarcation of nests in the compound structure, we cannot say unequivocally that birds contributed only to their own nest. There is also overt conflict between pairs, with stick theft common among neighbours, despite successful defensive behaviour by residents against kleptoparasitic conspecifics.

Our results suggest that there are specific sex-roles in the building and maintenance of monk parakeet nests, males contributing most to nest building and females to nest defence. We conducted our observations during the breeding season, so it is possible that females built less because they were incubating eggs or brooding young chicks, both of which are exclusively female activities (Eberhard 1998); their presence at the nest may also predispose them to defend against kleptoparasites. However, Eberhard (1998) also reported that females contributed little to nest-building during the pre-laying period, so it seems likely that there is also task specialisation between the sexes when not breeding. Such specialisation in reproductive roles between the sexes is, of course, widespread, including

in building activity in other communally nesting species (e.g., Winterbottom et al 2001, van Dijk et al 2014).

Nest building is a costly activity (Mainwaring and Hartley 2013) and may be especially so for the monk parakeet because their nests are maintained throughout the year (Eberhard 1998) and can be very large; a nest in our study population containing just two nest chambers was estimated to weigh 100 kg and contain approximately 10,000 sticks (JC Senar, unpublished data). Group-living may reduce the cost of nest-building because individuals breeding in groups delivered fewer sticks to the nest compared to those in pairs, although the same pattern was not observed for nest maintenance behaviours. This indicates a 'load-lightening' effect of extra group members (Crick 1992, Hatchwell 1999) that has been shown to result in increased survival (Meade et al 2010) or lifespan (Downing et al 2021) in other cooperatively breeding species. Load-lightening may be particularly apparent in males as they invest most in nest-building, although there may also be specific load-lightening benefits for females in other aspects of reproductive investment, e.g., nestling provisioning. Young males that remain in a group may also benefit from acquisition of nest-building skills (Heinsohn 1991); indeed, improved nest-building ability has been identified as a specific skill acquired by helpers in Seychelles warblers *Acrocephalus sechellensis* (Komdeur 1996).

Another potential benefit of living in a group may be having more individuals to defend the nest from kleptoparasites, as we found that nest defence was effective in reducing loss of nest material, and sometimes involved multiple group members. Therefore, if frequent nest material kleptoparasitism by conspecifics or heterospecifics (Dawson Pell et al 2023) presents a significant challenge to nest integrity or to reproductive success, this may be mitigated in larger groups. Nest defence could also reduce losses from predators and potentially from conspecifics. We did not witness any

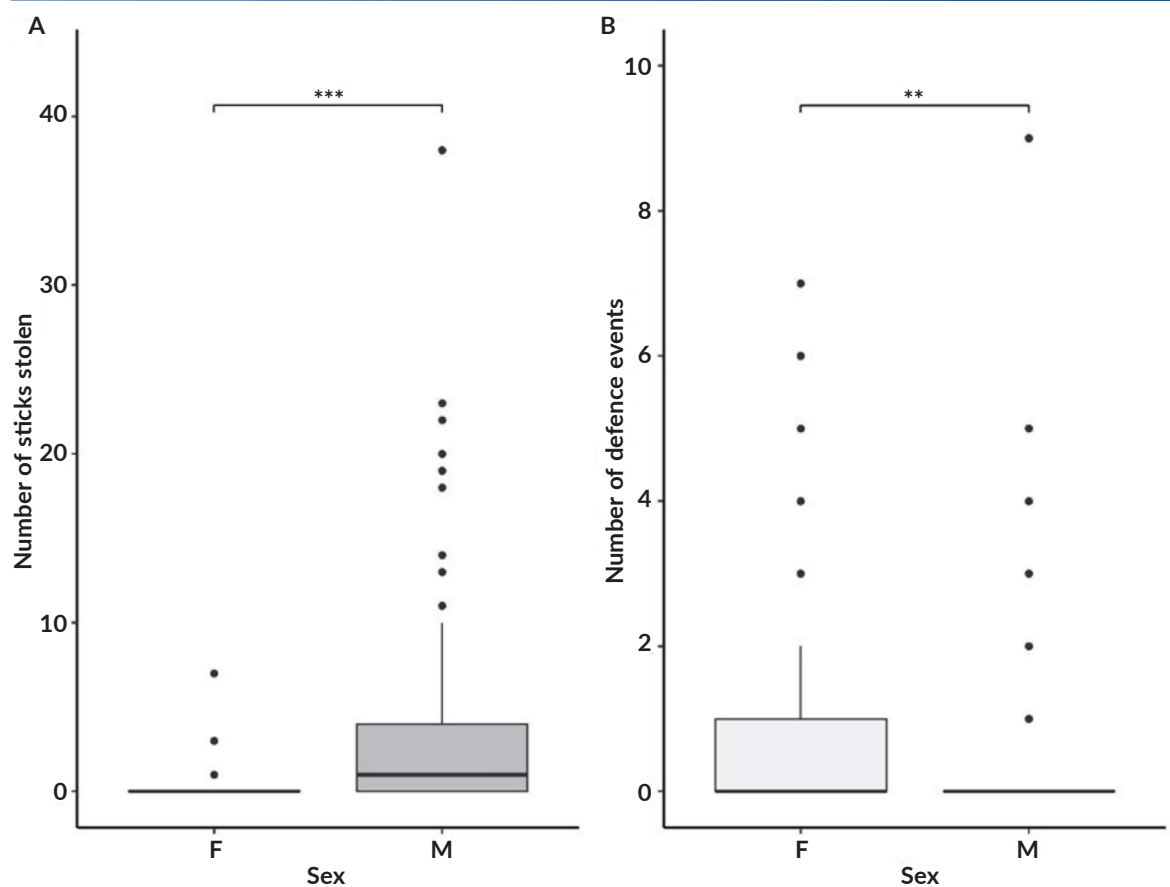


Fig. 2. Stick theft (A) and nest defence (B) behaviour by female (F) and male (M) monk parakeets. Data for all individuals shown for both years (N = 206 birds: 83 females, 123 males). Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). *** $p < 0.001$, ** $p < 0.01$.

Fig. 2. Comportamiento de robo de ramas (A) y defensa del nido (B) por hembras (F) y machos (M) de cotorra argentina. Se muestran los datos relativos a todos los individuos en ambos años (N = 206 aves: 83 hembras y 123 machos). En los diagramas de caja se indica el intervalo intercuartílico (límites superior e inferior de las cajas), la mediana (líneas gruesas dentro de las cajas), los niveles máximos sin contar los valores atípicos (líneas que se extienden fuera de las cajas) y los valores atípicos (puntos). *** $p < 0,001$, ** $p < 0,01$.

predation on monk parakeet eggs or nestlings during our observations, although rats *Rattus rattus* are sometimes seen at nests and are potential predators of eggs and young nestlings. Infanticide by neighbours occurs in other communally nesting species, such as the sociable weaver (R Covas, pers. comm.), and is frequent in some colonial bird species, especially seabirds (e.g., Forsy et al 2022). Infanticide resulting from reproductive competition within groups of co-breeders is also frequent in cooperatively breeding birds (e.g., Koenig et al 1995, Almstead et al 2020) and mammals (e.g., Young and Clutton-Brock 2006). It is speculated that adult monk parakeets occasionally kill nestlings (Peris and Aramburü 1995), but in this study we did not observe or suspect such behaviour.

The structure of the monk parakeet compound nest means that we cannot conclude unequivocally whether the nest is an emergent property of individuals investing building effort in their own nest chamber only, or whether structures are built and maintained through the cooperative investment of all nest oc-

cupants. Unlike the large compound nests of sociable weavers, in which nest chambers are embedded within a communal thatch (van Dijk et al 2014), there is no portion of the monk parakeet nest that would necessarily require equivalent cooperative investment. Moreover, the compound nests of monk parakeets have no clear demarcation between adjacent chambers and birds were regularly observed delivering sticks to areas of the nest that could not easily be assigned to a particular chamber (FSE Dawson Pell, pers. obs.). This suggests that some building may be characterised as mutually beneficial investment in the nest structure. In the sociable weaver, male kin are spatially clustered within compound nests and cooperative investment in the nest structure is kin-directed (van Dijk et al 2014). Male kin are similarly aggregated in the compound nests of monk parakeets (Dawson Pell et al 2021), so kin-selected cooperative construction and maintenance of their nests cannot be discounted. This is consistent with the growth of compound nests through a budding process as philopatric offspring build

additional chambers on to their natal nest (Dawson Pell et al 2021). Moreover, the lower frequency of compound nests in 2019, following the destruction of some nests as a pest control measure at the end of the 2018 breeding season, is also consistent with an incipient process of compound nest development. Conversely, there is evidently conflict among neighbours or potential neighbours over the construction of compound nests because of kleptoparasitism, and we also observed physical fights and vocalisations between residents and birds attempting to begin a new chamber on an existing nest (FSE Dawson Pell, pers. obs.). The precise balance of conflict and cooperation in compound nest construction in the monk parakeet, and the extent to which kinship mitigates conflict would be worth further investigation, especially in an unmanaged population where nests reach much larger sizes and house many more pairs (Spreyer and Bucher 1998, Burger and Gochfeld 2005).

In conclusion, the construction of stick nests and compound nest structures by monk parakeets is unique among parrots and has few parallels among other vertebrates, such as mound-building mice *Mus spicilegus* (Garza et al 1997), sociable weavers (van Dijk et al 2014) and red-billed buffalo-weavers (Winterbottom et al 2001), although it is widespread in some other social taxa, such as the Hymenoptera and Isoptera (Rubenstein and Abbot 2017). There are too few compound-nesting species to make any broad characterisation of the evolutionary route to compound-nesting among birds, but a broader perspective that includes these other taxonomic groups suggests that this behaviour may often be kin-selected, occurring primarily within family groups. However, systematic comparative analyses to examine this assertion is beyond the scope of the current study.

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Author contributions

FS Dawson Pell, BJ Hatchwell and JC Senar designed the study. FS Dawson Pell, A Ortega-Segalerva and JC Senar conducted the fieldwork, FS Dawson Pell conducted laboratory work and analysed the data. FS Dawson Pell wrote the paper with input from co-authors. All authors read and approved the final manuscript.

Conflicts of interest

No conflicts of interest declared.

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Complete affiliations

Francesca S. E. Dawson Pell, Ben J. Hatchwell, Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, S10 2TN, UK.

Juan Carlos Senar, A. Ortega-Segalerva, Museu de Ciències Naturals de Barcelona, Castell dels Tres Dragons, Psg Picasso s/n, Parc Ciutadella, 08003, Barcelona, Spain.