Ornis Fennica 92:157–171. 2015

Effects of experimental perturbation of group structure on hierarchy formation and behaviour in House Sparrows

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Received 8 June 2015, accepted 25 November 2015

Establishment of dominance hierarchies has been proposed as a mechanism that stabilizes and maintains social groups by reducing physical intra-group conflicts. However, the exact behavioural processes involved in hierarchy formation within natural populations, as well as those leading to destabilization, are still a matter of debate. Here, we investigate possible behavioural processes in play during periods of high and low social cohesion by experimentally manipulating group structure (experimental perturbation). House Sparrows (*Passer domesticus*) are an ideal study species as they form gregarious flocks structured by social dominance. Using a non-breeding flock of wild-caught urban sparrows, we analysed four behavioural parameters (outside the feeding context: agonistic behaviour; within the feeding context: non-aggressive joining, aggressive supplanting and the duration of feeding bouts) in relation to birds' sex and social rank during successive periods of unstable and stable group structure. In this population birds established a hierarchy quickly after initial group fusion but did not re-establish transitive relationships after a subsequent perturbation of group structure. Dominant birds consistently showed more frequent agonistic and supplanting behaviour than subordinates, irrespective of experimental condition. Likewise, the length of feeding bouts was unaffected by the experimental treatment. Thus, House Sparrows appear to be resilient to a certain degree to disruptions of social organization. However, female but not male House Sparrows selectively increased rates of non-aggressive joining during the latter period of social stability. Here, we highlight processes involved in the formation and re-formation of social hierarchies in natural populations that are exposed to frequent sources of instability.

1. Introduction

Group-living is a common trait shared by many diverse taxa. In their adaptation to social life animals must reconcile associated costs and benefits, and conflicts over reproduction or essential resources arise frequently. Severe conflicts may reduce group performance and hinder cooperation (Aureli *et al.* 2002); therefore, it is assumed that stabilizing mechanisms exist that maintain social groups by mitigating conflicts. One such proposed mechanism is the establishment of dominance hierarchies.

Hierarchies are termed linear or transitive if a group's top-ranking individual dominates all others, the second-ranking individual dominates all except the most dominant, and so forth (Martin & Bateson 2007). These linear hierarchies allow members of a social group to avoid excessive energy and time expenditure into repeated contests, and to reduce risk of injury or death (Clutton-Brock *et al*. 1986, Aureli & de Waal 2000). In such hierarchically structured groups high social rank determines priority of access to resources (Ekman & Askenmo 1984), leaving subordinates with less predictable access (Ficken *et al*. 1990, Polo & Bautista 2002). As such, dominant Willow Tits (*Poecile montanus*) and Coal Tits (*Periparus ater*) actively exclude subordinates from preferred foraging sites in winter flocks (Ekman & Askenmo 1984, Polo & Bautista 2002). Likewise, in Black-capped Chickadees (*Poecile atricapillus*), dominant birds are able to gain immediate access to resources by means of aggression, leaving subordinates to wait in the vicinity until the feeding site is unoccupied (Ficken *et al.* 1990). This discrepancy of food access alters subordinates' daily body mass management (Lange & Leimar 2004) and negatively affects birds' fitness in terms of survival, although it is likely that low-ranking birds may be even worse off outside the membership of a group (Ekman & Askenmo 1984).

Moreover, hierarchies remain stable only as long as group composition (Senar *et al*. 1990, Graham & Herberholz 2009) and environmental conditions do not change (Sloman *et al*. 2002). Surprisingly, it is still a matter of debate what mechanisms and behavioural processes are involved in establishing and maintaining hierarchies in natural populations (Dugatkin 1997, Valderrábano-Ibarra *et al*. 2007). Furthermore, where scarce experimental evidence exists, stabilizing factors seem to be inconsistent across social groups of different sizes (Chase & Seitz 2011) and at different times. Differences in individual attributes, for instance size and age asymmetries (Valderrábano-Ibarra *et al*. 2007), appear to play a large role during initial hierarchy formation and in dyadic encounters. On the other hand, social factors, among them trained winning and losing (Dugatkin 1997, Hsu *et al.* 2006) and bystander-effects (Dugatkin 2001, Chase *et al*. 2002), become more prevalent later on and in larger groups (Chase & Seitz 2011). In Blue-footed Boobies (*Sula nebouxii*), for example, ranks are initially assigned by differences in maturity between nest mates, which then give rise to differences in trained aggressiveness and submissiveness (Valderrábano-Ibarra *et al*. 2007), and in their later life birds continue to differ in rank due to this combination of persistent size asymmetries and trained winning and losing. No factor by itself, however, is likely to explain the process of hierarchy formation. Furthermore, the knowledge of processes that lead to the destabilization of hierarchies remains incomplete.

House Sparrows (*Passer domesticus* L. 1758) are an excellent model species for investigating social and dominance-related behaviour (e.g., Møller 1987, Liker & Bókony 2009). These gregarious songbirds spend much of their daily activity in year-round social groups (Andersson 2006), which are characterized by a complex and dynamic social system: large foraging aggregations usually comprise multiple tiers of subgroups (Haffer 1997) and fission-fusion events are common. Food discoveries of single individuals attract the attention of group mates quickly (Turner 1964) and sparrows may be remarkably skilled at obtaining social information. Outside the breeding season, the dominance structure in House Sparrow flocks is determined both by intrinsic (current testosterone titres and size of the male bib; Bókony *et al*. 2006, Nakagawa *et al*. 2007) as well as extrinsic features (history of previous dominance relationships; Buchanan *et al*. 2010). Female sparrows are generally regarded as being dominant over males during the breeding season (Haffer 1997) and in autumn flocks (Hegner & Wingfield 1987), whereas the exact nature of the dominance structure in winter flocks appears to be not yet resolved (cf. Møller 1987, Liker & Barta 2001, Hein *et al.* 2003). Dominant birds are able to secure the qualitatively highest food patches, forcing subordinates to forage more opportunistically (Lendvai *et al.* 2006) and under a greater threat of starvation (Polo & Bautista 2002).

Here, we were interested in determining the behavioural processes (patterns of social interactions) involved in the establishment, maintenance and destabilization of social organization. To this end, we used a flock of wild-caught urban House Sparrows and experimentally altered group composition under laboratory conditions: manipulation of the social environment such as the targeted removal of conspecifics has previously been recognized as a valid approach for testing assump-

Table 1. Study subjects. Subjects are ordered by social rank (standardized MDS: Modified David's score), starting from top rank in descending order. MDS was measured during the S1 condition (stability period 1: weeks 2–3). Corresponding rank classes were categorized as high (MDS: 0.6–1), intermediate (MDS: 0.3–0.6) and low (MDS: 0–0.3). Bold font indicates experimentally removed individuals (see text for details of the procedure). Not listed here is one experimentally removed bird (a high-ranking female from population 1; weight at capture: 27.3 g) that died in the last week of experiments. Capture sites within Turku, Southwest Finland, are: Sirkkala (population 1), Kärsämäki (population 2) and Muhkuri (population 3).

Subject	Native population	Sex	Weight at capture [g]	Weight at release [g]	Standard MDS	Rank class
H	**1**	**male**	**28.6**	**29.6**	**1**	**high**
I	2	male	30.8	30.5	0.696	high
EL	1	male	31.5	29.3	0.658	high
FA	2	male	34.0	28.8	0.647	high
T	1	female	31.2	29.4	0.616	high
FE	1	male	31.0	31.0	0.592	intermediate
R	1	female	31.7	29.7	0.539	intermediate
B	**2**	**male**	**33.8**	**31.0**	**0.502**	**intermediate**
D	3	male	30.8	29.6	0.495	intermediate
GF	2	male	32.3	29.3	0.357	intermediate
EW	2	female	34.5	30.4	0.332	intermediate
M	1	female	32.0	29.4	0.271	low
S	2	female	33.2	28.3	0.240	low
EM	2	male	35.8	31.3	0.222	low
L	1	male	34.3	31.0	0.072	low
A	2	male	33.5	29.7	0	low

tions about the underlying group structure (Krause & Ruxton 2010, Croft *et al*. 2011, Pinter-Wollman *et al*. 2014). To our knowledge, experimental studies investigating social dynamics in wild animals, especially in birds, are still underrepresented in the scientific literature.

In our study, perturbation of group composition occurred twice: first, during the initial mixing of previously unfamiliar birds from different sampling sites, and second, during experimental removal and reintroduction of conspecifics. We then analysed birds' behavioural responses (agonistic behaviour, non-aggressive joining, aggressive supplanting and the duration of feeding bouts) in relation to their sex and social rank during successive periods of unstable and stable group structure. We hypothesized that (a) experimental perturbation would result also in structural instability, i.e., dominance hierarchies are expected to become intransitive (non-linear) during perturbation treatments. We further hypothesized that (b) experimental perturbation affects dyadic interaction patterns between flock mates: during periods of social stability we expected dominant birds to engage more frequently in aggressive behaviour than low-ranking conspecifics, as social rank relationships are presumably linear and most predictable. Since dominant sparrows also gain priority access to food (Lendvai *et al*. 2006), we expected supplanting rates and the length of feeding bouts to be elevated compared to subordinates during stable periods. During periods of instability, on the other hand, we assumed to find no differences in aggressive dyadic interaction rates between social rank classes. Further, as female sparrows dominate males in the autumn (Hegner & Wingfield 1987), females were expected to show aggressive behaviour more frequently than males.

2. Material and methods

2.1. Subjects and housing

Between late October and mid-December 2012 we observed the behavioural responses of 16 wild-caught House Sparrows (five females, eleven males; Table 1) to manipulations of their social environment under controlled conditions. One additional bird (a dominant female) was initially part of the group but died in the last week of experiments due to coccidian infection of the gut. The bird was consequently excluded from behavioural analyses. After the experiments, the birds were released back into the wild (see below). The overall survival rate until release was considerably high (94%, i.e., 16 out of 17 birds survived).

One week prior to data collection birds were caught from natural habitats in the city of Turku, Southwest Finland (60°27' N, 22°16' E), and were subsequently housed as one social group in an indoor aviary at the Botanical Garden of Turku University. Birds were captured on four consecutive days and from three urban sites, located > 4.5 km apart from each other. Eight birds (four males) were captured in Sirkkala in central Turku, another eight birds (six males) were captured from the open storage area of an agricultural supermarket in north-eastern Kärsämäki, and a single male was caught in north-western Muhkuri (Table 1). Sirkkala and Muhkuri are small house areas with a comparatively high vegetation cover, while Kärsämäki constitutes mainly industrial area interspersed with green spaces and forests. Mist nets and baited live traps were used for capturing birds.

By sampling birds from different locations and combining them into a single flock we intended to experimentally simulate fission-fusion dynamics in wild autumn and winter flocks. Previously established dominance hierarchies were probably disrupted during sampling. Moreover, we consider birds sampled from different sites to be entirely naïve towards each other and, consequently, birds had to establish new social relationships. We note that no breeding was interrupted during the course of the study. Upon capture birds were sexed, weighed and marked with plastic colour-rings for individual identification. Sex could be determined without error due to sex-specific plumage characteristics (males: crest ash grey with a brown band framing the eye, wings sporting a conspicuous white wing band, after the autumnal moult with a variable black patch (bib) on throat and chest; females: head and body uniformly yellow-brownish and lacking the wing band; Haffer 1997). All birds possessed the fully matured plumage of adults, with the exception of one male (FA; Table 1) who was estimated to be in his first year of life.

Subjects were transferred to the housing facilities immediately after capture. Birds were housed together as one flock in an indoor aviary (L: 5.20 m; B: 2.44 m; H: 2.42 m) outfitted with two feeding platforms (L: 121 cm; B: 59 cm; H: 85 cm), a small sand box for dust bathing and several perching branches and platforms mounted to the walls at various heights. Social interactions and feeding behaviour were observed through a Plexiglas window facing the main feeding platform. The window could be covered entirely with opaque cloth except for a small circular hole to point a video camera lens. The aviary also contained a side compartment (L: 2.10 m; B: 1.00 m; H: 2.42 m) with one feeding platform and perching branches, which was used to house experimentally removed subjects (see below). The compartment was demarcated by opaque heavy cotton curtains fastened to the walls and ceiling, which provided efficient physical and visual barriers for the birds but allowed limited vocal communication. Importantly, birds in the main and side compartments were unable to interact physically with each other. Lastly, both main room and side compartment contained ventilation openings as well as sheltering spots that the birds could visit (hedges built from natural branches). The sheltering spots also served as night roosts. Birds were housed at a light : dark period of 8:16 h, representative of natural conditions at the time of capture, and a constant temperature of 14°C during daytime and 10°C during the night. *Ad libitum* access to water was provided at all times.

In mid-December, birds were released back into the wild at one site of previous capture (Sirkkala in central Turku). Study subjects were deemed to be well acquainted with each other and were hence released together. Prior to their release, the indoor temperature was gradually adjusted to acclimatize the birds to outdoor conditions. Birds were weighed again at approx. the same time of day as during their initial capture (10–12 a.m.). We found a significant decrease in mean body weight between the birds' capture and release dates (paired-samples t-test: $t = 5.681$, $p < 0.001$, $N = 16$; capture: 32.1 ± 2.2 g (mean ± SD), release: 29.9 ± 0.9 g; SPSS Statistics 20.0, IBM). The dominant female that died during the last week of study (see above) was excluded from weight analyses. The observed weight loss corresponds to 7.6 ± 5.3% of birds' body weight and was likely caused by a reduction in body fat: it has been shown that birds reduce body reserves under conditions of highly predictable foraging success (Ekman & Hake 1990), as is usually the case in captivity (Krams 2002). Therefore, over the course of one week additional wintering food for passerine birds was provided at the release site.

2.2. Experimental design

After the last individual was captured, birds were given three days to habituate themselves to their novel artificial surroundings. On the first day of data collection individuals were familiar with each other for a period of 3–6 days (mean: 4.65 ± 0.79 d). During this time the top and bottom ranks had presumably stabilized (cf. Verbeek *et al*. 1999, Lange & Leimar 2004). However, the establishment of a linear hierarchy was yet unlikely: in captivity, small groups of naïve House Sparrows may need at least one week to establish dominance (Hegner & Wingfield 1987).

Behavioural data were then collected during a six-week period, comprising four consecutive experimental conditions: perturbation period 1 (P1), stability period 1 (S1), perturbation period 2 (P2) and stability period 2 (S2). During the first experimental condition (P1), semi-naïve birds were permitted to establish novel social ties, allowing a reorganization of social structure. The P1 condition lasted for one week, after which an initial hierarchy had presumably been established (Hegner & Wingfield 1987). In the following S1 condition, lasting for two consecutive weeks, group composition remained constant. At the beginning of week four we caught three randomly predetermined individuals out of the group. Birds were flushed out of their cover into a mist net, which allowed for quick handling and kept stress responses to a minimum. Experimentally removed birds were one dominant male and one male of intermediate rank (Table 1; demarcated in bold) as well as one later deceased dominant female (not included in behavioural analyses; see above). The targeted individuals were released together into the aviary's side compartment and all birds were provided with excess food. Housing the birds together in the side compartment ameliorated effects of social isolation and limited vocal contact with the remainder of the group was possible at all times. The removal interval lasted for ten days in total, during which no data were collected. During this period, ensuing within-group struggles over vacant rank positions in the main group were likely (cf. de Waal 1977). After ten days the side compartment was opened in the evening, 1 h before lights went out, and the removed individuals re-joined the group. Data collection commenced the following day for the duration of one week (the P2 condition), as group members were expected to re-establish social rank order once more. Finally, data were collected for one more week characterized by constant group composition and an assumed stable group structure (the S2 condition).

2.3. Data collection

Behavioural data were collected on five days of the week in each condition. In the mornings birds were food-deprived for the first 1.5 h of daylight (8:15–9:45 a.m.). One container with food (L: 23 cm; B: 15 cm; H: 7 cm; winter seed mix for passerines) was then placed in the centre of the feeding platform, after which dyadic interactions and feeding bouts were recorded continuously for a total duration of 20 min, starting from the moment when the first bird landed on the platform. Feeding from the container ensued quickly (mean latency to feed: 52.4 s; range: 10–343 s). The first feeding bout after food deprivation is the most relevant for observations of dominance-related behaviour, since starvation risk in the mornings is high for birds. Consequentially, aggression between flock members is greatly increased (Andersson & Ahlund 1991, Polo & Bautista 2002). Recording was done using a digital HD video camera (Sony Handycam) pointed at the platform from the opposite window. The birds were unable to see the experimenter during data collection. Importantly, all social interactions between birds were observed solely on top of the feeding platform. After data collection, an additional container with *ad libitum* food was provided to enable all birds to feed regularly for the rest of the day.

We recorded the frequency of dyadic social interactions (Table 2) in addition to the length of feeding bouts, i.e., the time [in sec] of actively feeding from the food container. Only behavioural parameters involved in agonistic conflicts (e.g.,

Table 2. Definitions of behavioural parameters. Parameters within each category significantly correlate with each other (Mantel tests with sequential Bonferroni corrections; 10,000 permutations each).

Category	Parameter	Definition
Agonistic interactions	Displacement	An individual approaches a conspecific without physical aggression and the recipient immediately flees
	Agonistic displacement	An individual approaches and physically attacks (pecks) a conspecific; the recipient immediately flees
	Threat display	An individual approaches a conspecific with outspread wings (males display wing bars), in pecking stance, occasionally flipping of the tail
	Fight	An individual attacks a conspecific in flight, repeatedly pecks, tries to overturn the contestant; the recipient is defeated and retreats
	Chase	An individual chases after a fleeing conspecific, in pecking stance
Joining interactions	Tolerated scrounging	An individual approaches a feeding conspecific without conspicuous agonistic behaviour; both feed together in close proximity (within pecking distance)
Supplanting interactions	Supplanting	An individual approaches a feeding conspecific without physical aggression and the recipient immediately flees, giving up the resource
	Agonistic supplanting	An individual approaches and physically attacks (pecks) a feeding conspecific; the recipient immediately flees, giving up the resource
	Supplanting attempt	An individual approaches and physically attacks (pecks) a feeding conspecific but receives retaliatory aggression; the recipient does not leave immediately

fights, displacements and threat displays; no involvement of food items) and those aimed at gaining access to food (scrounging behaviour; involving food items) were analysed. A further distinction was made between non-aggressive scrounging (feeding next to conspecifics, hereafter termed joining) and aggressive scrounging (taking over a feeding spot by displacing conspecifics, hereafter termed supplanting). This yielded three behavioural categories: (a) agonistic interactions, (b) joining interactions and (c) supplanting interactions. Within each such defined category we employed matrix correlations to test whether corresponding parameters correlated with each other (Mantel tests with sequential Bonferroni corrections, 10,000 permutations each; MatMan 1.1 by Noldus Technologies, de Vries *et al*. 1993). Only those parameters that correlated significantly with each other (Table 2) were pooled for further analyses. Parameters were then corrected for sampling effort, i.e., individual variation in the time observed on the feeding platform, and standardized to 1 min observation time. On average, birds were observed on the platform for 79.9 ± 36.0 min / individual ($N = 16$) over the course of the study, during which we counted a total of 1,815 agonistic interactions, 674 joining interactions and 717 supplanting interactions.

2.4. Social rank and dominance hierarchies

We assessed birds' social ranks by calculating David's scores (David 1987) in the S1 condition. David's score indexes an individual's wins and losses against each of the other group members, weighted by an estimate of the overall strength of the respective contestant (de Vries *et al*. 2006). Here, we implemented de Vries *et al*.'s (2006) modified version of David's score (hereafter MDS), which also takes unevenly distributed interactions between individuals into account. MDS was calculated from an assay of five strongly asymmetric agonistic parameters (Chase & Seitz 2011) that correlate significantly with each other: displacement, agonistic displacement, agonistic supplanting, fight and chase (see Table 2 for definitions). The S1 condition was chosen because sparrows had presumably established a stable hierarchy by this point: Whitehead (2008) recommends assigning individual ranks only when dominance hierarchies are linear. This assumption was met as condition S1 fitted a linear hierarchy well (de Vries's test for linearity of hierarchies: h': 0.347, $p = 0.003$, $N = 16$; 10,000 permutations).

In a next step, we standardized MDS to values between 1 (most dominant) and 0 (most subordinate). Based on these standardizations individuals were categorized as being either dominant (MDS: 0.6–1), of intermediate rank (MDS: 0.3–0.6) or subordinate (MDS: 0–0.3; Table 1). Social rank was then used in mixed within-between subjects ANOVA (see below) as an ordinal scale explanatory variable. In addition, we tested whether a linear hierarchy was present in each of the experimental conditions using a randomization test (de Vries 1995). The program SOCPROG 2.5 (Whitehead 2009) was used for calculating MDS and for testing linearity of hierarchies.

2.5. Statistical analysis

Data were analysed with mixed within-between subjects (or: mixed design) ANOVA. This design combines factorial analysis with repeated-measures analysis. Continuous scale response variables comprised mean rates of agonistic interactions, joining interactions and supplanting interactions, as well as the mean duration of feeding bouts. Interactions were measured as the frequency of occurrence of distinct behaviours, averaged over group members. Both interaction frequencies and feeding durations were corrected for individual sampling effort. Discrete scale explanatory variables in the initial models were Condition (the within-subjects variable) and either Sex or Social Rank (the between-subjects variables). Condition delineates the experimental treatment, i.e., the P1, the S1, the P2, and the S2 condition. Agonistic and supplanting interaction rates were $\log_{10}$-transformed prior to analyses to fulfil assumptions of normality. Equality of covariance was assumed if Box's test was non-significant at an alpha level of 0.001. In case the assumption of sphericity was violated, i.e., Mauchly's test yielded a $p \leq 0.05$, we used the Greenhouse–Geisser correction of F-ratios in order to estimate sphericity (Greenhouse & Geisser 1959). Models contained either Condition and Sex as the explanatory variables, or Condition and Social Rank, but due to a sample size of $N = 16$ it was not feasible to analyse Sex and Social Rank in conjunction. For each response variable we then selected the model with the better fit to the data, implementing the corrected Akaike information criterion (AICc; designed for small samples), and rejected the other. In case the within-subjects variable (Condition) reached significance (either as an interaction or main effect), we carried out planned comparisons in the form of repeated contrasts. In case the between-subjects variable Rank reached significance as a main effect, we conducted Post-hoc tests between levels of Social Rank and applied sequential Bonferroni corrections (Holm 1979) to control for multiple comparisons. All statistical analyses were conducted with SPSS 20.0 (IBM).

3. Results

3.1. Dominance hierarchies

The flock of House Sparrows formed a moderately strong, linear dominance hierarchy already during perturbation period 1 (P1; h': 0.485, $p < 0.001$, $N = 16$; 10,000 permutations). Stability period 1 (S1) showed a moderately strong, linear hierarchy as well (h': 0.347, $p = 0.003$, $N = 16$; 10,000 permutations). Hierarchies during both perturbation period 2 (P2) and stability period 2 (S2) were non-linear and weak, however (P2: h': 0.179, $p = 0.329$, $N = 16$; S2: h': 0.290, $p = 0.076$, $N = 16$; 10,000 permutations each).

3.2. Quantitative behavioural responses to experimental perturbation

3.2.1. Effects of Social Rank

As a main effect Social Rank significantly influenced rates of both agonistic interactions and sup-

Table 3. Quantitative behavioural responses to experimental perturbation. Mixed within-between subjects ANOVA; N = 16. Models contained either (a) Social Rank and Condition, or (b) Sex and Condition as explanatory variables. The model containing Agonistic interactions as the response variable and Sex and Condition as the explanatory variables was rejected due to violations of the equality of error variances (see section 3.2.2.). Social Rank was measured during the S1 condition (stability period 1: weeks 2–3). Partial η^2 (partial eta squared) denotes the effect size. ΔAICc (the corrected Akaike information criterion) denotes a model's goodness-of-fit; listed is the deviance (Δ) from the optimal model (0 denotes the optimal model). †: error degrees of freedom in brackets. Significant results are marked in bold. Asterisk indicates significance (two-tailed): *: $p \le 0.05$; **: $p \le 0.01$.

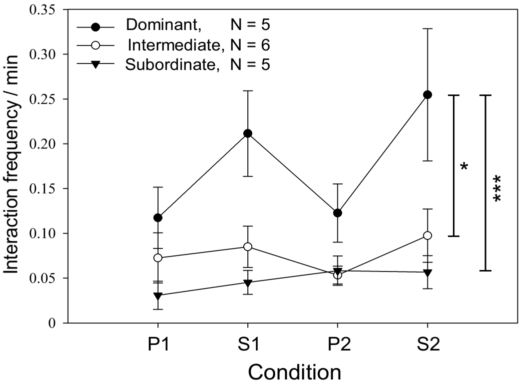
a)	Response variable	Explanatory variables	*F*	df †	*p*	Partial η^2	ΔAICc
	Agonistic interactions	Condition	3.472	1.69 (21.95)	0.056	0.211	0
		Rank	**8.376**	**2 (13)**	** **0.005**	**0.563**	
		Condition × Rank	0.581	3.38 (21.95)	0.653	0.082	
	Joining interactions	Condition	1.399	3 (39)	0.257	0.097	24.54
		Rank	**4.123**	**2 (13)**	* **0.041**	**0.388**	
		Condition × Rank	**2.349**	**6 (39)**	* **0.049**	**0.265**	
	Supplanting interactions	Condition	1.176	1.63 (21.24)	0.319	0.083	0
		Rank	**4.096**	**2 (13)**	* **0.042**	**0.387**	
		Condition × Rank	1.287	3.27 (21.24)	0.305	0.165	
	Feeding duration	Condition	0.500	1.51 (19.62)	0.563	0.037	0
		Rank	1.810	2 (13)	0.203	0.218	
		Condition × Rank	0.923	3.02 (19.62)	0.448	0.124	
b)	Response variable	Explanatory variables	*F*	df †	*p*	Partial η^2	ΔAICc
	Agonistic interactions	–	–	–	–	–	–
		–	–	–	–	–	
		–	–	–	–	–	
	Joining interactions	Condition	2.421	2.05 (28.64)	0.106	0.147	0
		Sex	3.925	1 (14)	0.068	0.219	
		Condition × Sex	**3.724**	**2.05 (28.64)**	* **0.036**	**0.210**	
	Supplanting interactions	Condition	1.072	1.74 (24.33)	0.350	0.071	4.07
		Sex	0.130	1 (14)	0.724	0.009	
		Condition × Sex	1.030	1.74 (24.33)	0.363	0.069	
	Feeding duration	Condition	0.392	1.57 (22.03)	0.631	0.027	26.57
		Sex	0.007	1 (14)	0.936	0	
		Condition × Sex	0.307	1.57 (22.03)	0.687	0.021	

planting interactions, with large effect sizes (56.3% and 38.7% variance explained, respectively; Table 3a).

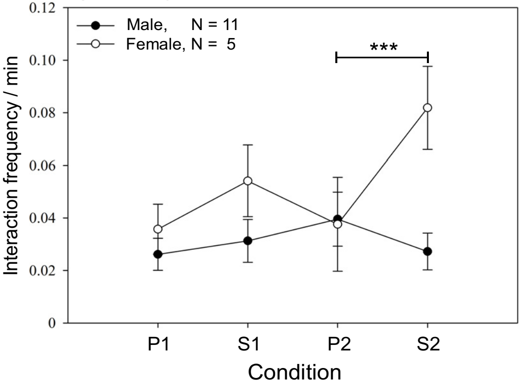
Sparrows of high social rank interacted agonistically more frequently than birds of intermediate rank (mean ± SE: high rank: 0.177 ± 0.027; intermediate rank: 0.077 ± 0.012; Post-hoc *t*-test: t_{13} = 2.667, p = 0.019, N = 11; Fig. 1a) or their low-ranking conspecifics (low rank: 0.048 ± 0.008; t_{13} = 4.041, p = 0.001, N = 10).

Similarly, dominant sparrows supplanted conspecifics more frequently than did birds of intermediate rank (high rank: 0.061 ± 0.009; intermediate rank: 0.031 ± 0.005; t_{13} = 2.154, p = 0.051, N =

a) Agonistic behaviour



b) Joining



c) Supplanting

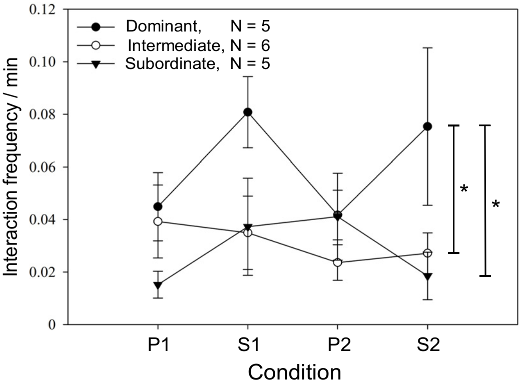


Fig. 1. Frequencies of (a) agonistic interactions, (b) joining interactions and (c) supplanting interactions per min observation time. Mean ± SE; $N = 16$. Plots show (a, c) social rank classes (see text) and (b) sexes. Repeated contrasts between conditions; Post-hoc test with sequential Bonferroni corrections between levels of social rank. Back-transformed values (a, c) used for purposes of clarity. P1: perturbation period 1; S1: stability period 1; P2: perturbation period 2; S2: stability period 2. Asterisk indicates significance (two-tailed): *: $p \leq 0.05$; ***: $p \leq 0.001$.

11; Fig. 1c) or subordinate birds (low rank: 0.028 ± 0.007; $t_{13} = 2.732$, $p = 0.017$, $N = 10$).

3.2.2. *Effect of Sex*

We initially discovered an interaction effect between Sex and Condition on the rates of agonistic interactions. However, homoscedasticity, i.e., the assumption of equal error variances, was violated in the S1 and the S2 condition, which impacted resulting F-ratios. We were unable to correct for this violation of assumptions and rejected the model as a consequence.

Both, Social Rank in interaction with Condition as well as Sex in interaction with Condition, impacted rates of joining conspecifics at the feeder (Table 3a, b); however, the interaction between Social Rank and Condition fitted the data considerably less well (ΔAICc = 24.54; Table 3a) and was therefore rejected.

The interaction effect between Sex and Condition was significant, with a small effect size (21.0% variance explained; Table 3b). Sexes differed in observed joining interaction rates in the transition from perturbation period 2 toward stability period 2 (repeated contrast: $F_{1, 14} = 11.355$, $p = 0.005$): female sparrows joined conspecifics at the feeder significantly more frequently during the S2 condition compared with the P2 condition (P2: 0.038 ± 0.018; S2: 0.082 ± 0.016; increase from P2 to S2: $F_{1,4} = 68.464$, $p = 0.001$; Fig. 1b). For males, no such pattern was detected (P2: 0.040 ± 0.010; S2: 0.027 ± 0.007; $F_{1, 10} = 1.286$, $p = 0.283$).

3.2.3. *Effect of Condition*

We found a marginally significant effect of Condition as a main effect on rates of agonistic interactions (Table 3a). When Social Rank, the between-subjects variable, was dropped from the models, however, the main effect of Condition became significant ($F_{1.76, 26.42} = 3.593$, $p = 0.047$, partial $\eta^2 = 0.193$). Doing so did not notably deteriorate the model's goodness-of-fit (ΔAICc = 1.845). Birds displayed significantly more frequent agonistic interactions in their transition from perturbation period 1 to stability period 1 (P1: 0.074 ± 0.017; S1: 0.112 ± 0.024; increase from P1 to S1: $F_{1, 15} = 5.844$, $p = 0.029$).

Neither Condition nor Social Rank or Sex, as main effects or in an interaction, had a notable effect on the duration of birds' feeding bouts throughout the experiments (Table 3a, b).

4. Discussion

In this study, captive House Sparrows developed a moderately linear social hierarchy over the first two experimental conditions (perturbation period 1 and stability period 1). However, hierarchies destabilized at the onset of perturbation period 2 and linearity was not reached again during stability period 2. These findings are in part surprising: while sparrows formed a stable hierarchy during the S1 condition as could be expected, dominance relationships did not stabilize again after a second perturbation (in the S2 condition), indicating a structural destabilization within the flock. Departure from linearity, in response to the experimental perturbation, was expected in the P2 condition as birds were assumed to re-establish rank order. Conversely, birds established transitive dominance relationships early on, already during the first week of experimentation after birds from different flocks had been fused into one social group.

Thus, while our group of House Sparrows was faster than expected in generating a dominance hierarchy, they were unable to re-establish rank after a second perturbation. These findings may indicate that the robustness of hierarchies can be challenged by invasive changes in group composition, depending, perhaps, on the nature of the removed / introduced individuals and the social niches they had occupied. Here, we experimentally removed birds of high and intermediate social rank; however, in the framework of this study we cannot distinguish between the effects the removal of high-ranking birds has on the behaviour of group mates over, for instance, the removal of subordinates.

This question has been investigated in a seminal study by Flack and colleagues (Flack *et al.* 2005) who used a perturbation technique to study the robustness of social structure in a group of captive Pigtailed Macaques (*Macaca nemestrina*), a primate with complex triadic relationships. Three top-ranking males were repeatedly (once every two weeks during a 20-week study period) separated from their social group for several hours. The males were known to engage disproportionately in conflict management interactions (Flack *et al.* 2005). The perturbation regime was meant to imitate natural fluctuations in group composition due to disease and predation. Destabilization of the social system occurred without the presence of conflict managers as conflicts and aggressive interactions increased in frequency while affiliative behaviour (e.g., play, grooming and contact sitting) and the functioning of conflict repair mechanisms were greatly reduced (Flack *et al.* 2005).

Our study differs from the experimental design of Flack *et al.*'s (2005) study in that we did not remove subjects repeatedly. In addition, House Sparrows face a far greater risk of predation (e.g., Bell *et al.* 2010), among other differences in ecology. We would still expect group members to re-establish dominance relationships in a reasonable time following experimental removal and reintroduction (the P2 condition), i.e., after one week (Hegner & Wingfield 1987). However, this could not be observed in the subsequent S2 condition.

Alternatively, our findings might indicate that House Sparrows are able to maintain stable hierarchies only for relatively short periods of time, before natural or population-dynamic processes reintroduce structural instability. Watson (1970) reported that in captivity intransitive hierarchies can be a common feature in House Sparrow groups, because subordinates successfully displace higher-ranking conspecifics from time to time. Captivity naturally prevents birds' inclinations for dispersal, which may affect their realized social system. In natural, free-moving groups of House Sparrows, on the other hand, fission and fusion of subgroups may be a common event as birds travel between feeding sites (Summers-Smith 1954, Beer 1961). In such societies, animals travel frequently between groups as an adjustment to the distribution of resources or as a means to reduce scramble competition (Chapman *et al.* 1995, Lehmann *et al.* 2007), and group composition may vary frequently and rapidly (Kummer 1971). These perpetual fluctuations would naturally pose a challenge to group cohesiveness. Liker *et al.* (2009), on the contrary, found that during a 2-month observation period of wintering flocks of House Sparrows over two consecutive years only about 16.5% of birds frequented more than one feeding site per year. In addition, House Sparrows do not normally disperse far from their natal site (Summers-Smith 1963, Andersson 2006), although this may depend on the spatial scale investigated (cf. Fleischer *et al.* 1984). These latter studies implicate that the House Sparrow social system is dynamic only at a rather small (local) scale, and is not prone to excessive amounts of instability.

In this study, we also investigated the effects of experimental perturbation of group composition on social interaction patterns and the length of feeding bouts. In line with expectations, dominant sparrows supplanted conspecifics and displayed agonistic behaviour more frequently than either subordinate birds or those of intermediate rank. However, they did so consistently over the course of the study, as the experimental treatment had no notable effect on dominants' aggressive behaviour. Rather, we observed an overall increase in group mates' agonistic interaction rate as the flock entered stability period 1, during which social ranks had presumably fortified. Moreover, and contrary to predictions, social rank did not affect the duration of sparrows' feeding bouts and neither did the experimental treatment have any effect on feeding behaviour. Thus, House Sparrows may be robust to some degree to the (artificial) disruption of their social organization and do not seem to incur direct fitness costs in the form of reduced feeding times and, possibly, food intake. Along these lines, Ficken *et al.* (1990) found that also in winter flocks of Black-capped Chickadees social rank was not strongly related to access to a super abundant food source. In their study, subordinates were able to obtain food regularly but were more likely to wait until the feeder was unoccupied. Although not analysed here, we did observe a similar pattern in some of our low-ranking House Sparrows. It should be noted, however, that in the wild food sources can be expected to be depleted much faster than under laboratory conditions, and subordinate birds are likely facing a higher starvation risk (cf. Ficken *et al.* 1990).

Contrary to predictions, sexes showed similar rates of agonistic and supplanting behaviour. There was, however, a sex difference in non-aggressive joining: females joined conspecifics significantly more often during stability period 2 than during the preceding perturbation period 2. Males, on the other hand, displayed more or less consistent rates of non-aggressive joining over the course of the study without a significant difference between any consecutive conditions. These findings may be consistent with a study conducted by Tóth *et al.* (2009), in which the authors found that female House Sparrows used non-aggressive food scrounging more often and obtained more food from close kin than from unrelated birds. Males, on the other hand, were found to scrounge less often from kin. Although relatedness was not measured during the course of our study, it is possible that closely related birds were indeed present among flock mates sampled from either Kärsämäki or Sirkkala. However, Liker *et al.* (2009) found that most individuals in wintering flocks of sparrows had only a few close relatives in their native flocks (14.3 ± 0.6% of flock mates, or one out of seven birds). Thus, it seems rather unlikely that kinship would have a huge effect in our mixed flock, which consisted of eight birds from each of the Kärsämäki and Sirkkala sites (plus a single bird from a third location). It is noteworthy to point out that female joining interactions did not peak during stability period 1 in a similar way. Yet, during the S2 condition female sparrows may have adopted a joining strategy if they were either at a lower risk of receiving retaliatory aggression from male group mates, or if chances of accessing the food source were higher by joining conspecifics rather than supplanting them (we note that four of the five female sparrows were of intermediate or low social rank, and thus supplanting may not be an optimal foraging strategy).

Understanding the underlying factors that govern the establishment and maintenance of social organization in House Sparrows is of interest for the conservation of the species. House Sparrows are globally successful due to their close commensalistic relationship with humans (Andersson 2006, de Laet & Summers-Smith 2007) and in urban areas sparrows often constitute the most numerous and dominant species (Vuorisalo & Tiainen 1993, Jokimäki *et al.* 1996). Albeit their adaptation, House Sparrows across Europe are experiencing major population declines since the mid-1980s in both cities and rural habitats (de Laet & Summers-Smith 2007, Murgui & Macias 2010). The decline of House Sparrows and other passerines in rural areas is fairly well understood and is likely caused by agricultural intensification, leading to a simplification of the landscape (Donald *et* *al*. 2001, Hole *et al*. 2002). On the other hand, several potential causes for declining populations in urban habitats have been identified over recent years: poor nestling condition and survival due to an inadequate diet (Peach *et al*. 2008, Seress *et al*. 2012) which is presumably linked to the scattered distribution of critical resources in cities (Vangestel *et al*. 2010), high predation by raptors such as the Eurasian Sparrowhawk (*Accipiter nisus*) recolonizing urban habitats (Bell *et al.* 2010), an increase in urban land coverage (Chamberlain *et al*. 2007) and high concentrations of pollutants (Peach *et al*. 2008), among others.

Our study has three notable limitations. First, we investigated only a single flock of House Sparrows of 16 individuals. Second, the number of consecutive manipulations of group structure should ideally have been larger. Third, we were unable to draw direct conclusions as to the effect of the removed subjects' social rank on group structure, as this would have warranted a controlled approach of successive removals of distinct rank classes. This was beyond the scope of the present study.

In spite of these limitations we feel that the study highlights the potential behavioural processes that may play a role in the destabilization of group structure. However, it would be important to corroborate our findings in a setup with multiple groups and replicated targeted removals before general conclusions about the sociology of the species can be drawn. We look forward to future experimental studies that test further assumptions about dominance and social dynamics in animal groups. As such, it may be worthwhile to investigate whether urban and rural House Sparrow populations perform differently during targeted removal experiments, or in what ways other behavioural contexts, such as associational or affiliative behaviour, are affected.

Acknowledgements. This study complied with Finnish and local guidelines for the experimental treatment of animals. The Animal Experiment Board of Finland (ELLA) approved the treatment of animals (permit number: ESAVI/6504/04.10.03/2012) and permission for capturing birds in the wild was received from the Centre for Economic Development, Transport and the Environment of Southwest Finland (ELY Centre; permit number: VARELY/653/07.01/2012). Great care was undertaken to minimize suffering of the birds during the course of the experiments. This work was supported by the Maj and Tor Nessling Foundation (grant numbers 2012092, 2013059 and 2014501) and the Ella and Georg Ehrnrooth Foundation to R.J.K. We thank K. Norrdahl for procuring the license for the experimental treatment of animals and J. Nurmi for his help in capturing the birds. We further thank M. Pölkki, T. Holm, W. Velmala and two anonymous referees for helpful comments on an earlier version of this manuscript.

Ryhmärakenteen kokeellisen manipuloinnin vaikutus varpusparven sosiaaliseen arvojärjestykseen ja parvikäyttäytymiseen

Parven sisäinen sosiaalinen hierarkia vähentää yksilöiden välisiä konflikteja, ja edistää siten parven koossa pysymistä. Sosiaalisen hierarkian vakiintumiseen tai purkautumiseen vaikuttavia prosesseja luonnon populaatioissa ei kuitenkaan toistaiseksi tunneta kovin hyvin. Tutkimuskohteemme varpunen (*Passer domesticus*) on laji, jolle parveutuminen ja sosiaaliset hierarkiat ovat hyvin tyypillisiä. Tutkimuksessamme muokkasimme aviaariossa pesimäajan ulkopuolella elävän varpusparven koostumusta poistamalla siitä yksilöitä, ja palauttamalla ne jonkin ajan kuluttua takaisin parveen.

Tarkkailimme kokeen eri vaiheissa kunkin yksilön suhtautumista parvikumppaneihinsa sekä ruokinnalla että sen ulkopuolella. Erityistä huomiota kiinnitimme yksilön sukupuolen ja sosiaalisen aseman vaikutuksiin aggressiivisiin vuorovaikutuksiin, sosiaalisiin tilanteisiin hakeutumiseen ja ruokailun kestoon. Kokeen alkaessa parven sosiaalinen hierarkia muodostui nopeasti, mutta ei palautunut enää ennalleen poistokokeen päätyttyä yksilöiden palauttamisesta huolimatta. Koejärjestelystä riippumatta sosiaalisessa arvoasteikossa korkealla olevat yksilöt olivat muita aggressiivisempia ja syrjäyttivät niitä ruokinnalla. Ravinnonhankintaan käytetty aika ei muuttunut kokeen aikana. Naaraiden aggressiivinen käyttäytyminen väheni parven yhdessäolon pidentyessä. Kokeemme perusteella varpusparvea eivät haittaa erilaisista häiriötekijöistä johtuvat sosiaalisen rakenteen muutokset.

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