

Amy Haigh  · Ruth O’Riordan · Fidelma Butler

## Variations in aggression and activity levels amongst squirrels inhabiting low and high density areas

Received: 12 April 2017 / Accepted: 30 August 2017  
© The Ecological Society of Japan 2017

**Abstract** Variation in an individual animal’s behavioural traits has been observed in a wide range of species and is believed to have important fitness consequences. As part of a larger study, it was observed that squirrels occurred at different densities on a 315 ha island, and this subsequently led to variations in faecal cortisol metabolite levels. This study aimed to examine whether living at different densities would also lead to variations in activity and aggression levels and in their survival probability, breeding and body condition. In order to examine variations in activity and aggression, behavioural tests (open field test, mirror image stimulation, breath rates and struggle rate tests) were conducted on 32 individuals (15♀, 17♂), a total of 69 times. Activity in the wild was investigated through radio tracking. There was a significant correlation between the time a squirrel was active and in their aggressive behaviour during the behavioural tests, with more aggressive individuals also being more active. Squirrels in the low density area spent a greater proportion of time active and engaged in aggressive behaviour in the open field test but also moved further in the wild and had a lower breath rate and higher struggle rates. Squirrels in the high density area were the least aggressive, had a smaller home range and higher breath and lower struggle rates. However, this was found to have no effect on survival probability, breeding or body condition. These variations may be the result of sampling dispersing squirrels.

**Keywords** Aggression · Activity · Home range · Fitness · Stress · Tolerance

**Electronic supplementary material** The online version of this article (doi:10.1007/s11284-017-1506-8) contains supplementary material, which is available to authorized users.

A. Haigh (✉) · R. O’Riordan · F. Butler  
School of Biological, Earth and Environmental Sciences, University College Cork and Fota Wildlife Park, Carrigtwohill, Cork, Ireland  
E-mail: amyjoahaigh@yahoo.com  
Tel.: 00353 86 1536327

### Introduction

Behavioural traits are thought to have important fitness consequences (Boon et al. 2007; Minderman et al. 2009) and may be reflected in many aspects of an animal’s behaviour and ecology, including habitat use, interactions with conspecifics, and willingness to take risks (Boon et al. 2008). Such traits can determine how individuals cope with various environmental challenges by behavioural means (Møller, 2010), for instance, less aggressive individuals might do well in situations where low aggression is favoured, but poorly in competitive situations (Sih et al. 2004). The correlation of different behaviours mean that an individual’s behaviour is not infinitely flexible. “An individual cannot adjust its behaviour to perfectly match each situation, but behaves in a similar manner in many different types of situations” (Korpela et al. 2011). Even if most individuals exhibit limited plasticity and a poor ability to cope with environmental change, a species can still respond adequately to the change, if the species harbours substantial variation in behavioural types so that at least some individuals respond well (Sih et al. 2004). Therefore, no single specific behavioural phenotype is favoured by selection, as changing and unpredictable environmental conditions will favour different phenotypes. As a result, heterogeneous populations, with individuals of both bold and shy personalities exist, allowing for adjustment to variable selective forces (Møller 2010).

Sih et al. (2004) define behavioural syndromes as a combination of correlated behaviours. Behavioural syndromes may reflect a selection of combinations of behaviours that work well together in a certain habitat (Penke et al. 2007). Adriaenssens and Johnsson (2011) found support for behavioural syndromes in brown trout (*Salmo trutta*) with less explorative individuals being less aggressive and showing more flexible behaviour. Similarly, Both et al. (2005) suggested that slow exploring great tits (*Parus major*) may be better parents, because they respond more easily to environmental

change. Correspondingly, Reale et al. (2000), detected that docile and bold rams (*Ovis canadensis*) survived longer than indocile and shy rams.

Displays of individual aggression may also show seasonal variation and in the Columbian ground squirrel (*Spermophilus columbianus*), Betts (1976) observed that aggression was most frequent during breeding and lactation among males and females, respectively. In aggressive interactions amongst red squirrels (*Scuirus vulgaris*), heavier individuals won more often than lighter individuals, irrespective of their sex (Wauters and Dhondt 1989). However, while seasonal variation in aggression has been observed, Boonstra et al. (2008) found that both male and female red squirrels (*Tamiasciurus hudsonicus*) are highly aggressive in both the breeding and non-breeding season.

While Selonen and Hanski (2010) found that genetic variability is an important factor behind the dispersal of flying squirrels (*Pteromys Volans* L.), the tendency to disperse may also be correlated with personality traits (Hoset et al. 2011 but see Selonen and Hanski 2010 and Selonen et al. 2012) and studies have shown that individuals exhibit personality-dependent dispersal, meaning that dispersal tendency is associated with boldness, sociability or aggressiveness (Cote et al. 2010). Some juveniles leave their natal population in search of more socially attractive or dense populations, others will disperse in order to avoid crowded populations (Cote et al. 2008; Hoset et al. 2011). In female North American red squirrels (*Tamiasciurus hudsonicus*), increasing activity was associated with an increasing propensity to enter traps, to intrude on the territories of others, and to move farther from their own territory, all of which represent risk-taking behaviours (Boon et al. 2008).

Wauters and Lens (1995) observed that 16% of the female European red squirrels moved from the territories on which they first settled to adjacent, vacant, territories, and once females had acquired territories, which are essential for successful reproduction, they normally stay there for life. It has been suggested that male European red squirrel home ranges might be determined by the density and dispersion of females (Wauters and Dhondt 1992; Andren and Delin 1994), while female home range size, which is probably determined by food availability, might indicate the area requirements of an adult individual squirrel (Andren and Delin 1994). Wauters and Dhondt (1989) observed that survival was positively correlated with body weight with squirrels of high body weight, and larger fat-reserves, being better equipped to cope with stressful conditions than squirrels of lower body weight. Reproduction can also have a significant contribution to mortality. In sexually promiscuous mammals, female reproductive effort is mainly expressed through gestation, lactation, and maternal care, whereas male reproductive effort is mainly manifested as mating effort (Hoffman et al. 2008). Therefore in polygynous or promiscuous mammals, male mating effort can have significant costs due to the risks associated with dispersal, energy expenditure

for mate attraction displays or intrasexual competition, fighting, and increased exposure to predation (Promislow 1992). It is not surprising therefore that males are often found to have a higher mortality rate than females (Neuhaus and Pelletier 2001).

As part of a larger study on a population of European red squirrels, it had been observed that squirrels were spatially clustered in relation to resource availability, with consequential variations in squirrel density (Haigh et al. 2015). This consequently also led to variations in faecal cortisol metabolites, with levels being higher in the high density wildlife park than the low (golf course) and medium density (gardens) areas (Haigh et al. 2017). As a follow on from these previous studies, this research aimed to examine whether other variations were manifest amongst these squirrels. For instance, with some squirrels living in close contact with conspecifics and others having more limited contact, did variations exist in their levels of aggression? Furthermore, with a clustering of individuals observed in the resource rich (high density) area (Haigh et al. 2015), did this lead to variations in activity, survival probability and body condition between the three areas?

---

## Materials and methods

### Study site

The study was carried out between February 2012 and March 2014 on an island (51.889585°N, 8.311276°W), 16.7 km from Cork City, Ireland and connected to the mainland by bridge on both sides. The 315 hectare island consists of a wildlife park (high density area, 32 hectares), a stately home and gardens (medium density area, 29 hectares), and an 18 hole golf course and resort (low density area, 243 hectares). An additional 11 hectares of land is currently being developed to expand the wildlife park (Fig. 1). In the wildlife park there is a total of 26 tree species, comprising mainly the native species *Quercus robur* (oak), *Salix caprea* (willow), *Betula pendula* (birch), *Alnus glutinosa* (alder) and *Pinus sylvestris* (Scots pine), with non-native species of *Fagus sylvatica* (beech), *Castanea sativa* (sweet chestnut), *Acer pseudoplatanus* (sycamore), *Larix x eurolepis* (larch), *Taxus baccata* (yew). The gardens have 130 tree species and varieties representing 26 genera, including *Pinus*, *Picea*, *Cupressus*, *Cryptomeria*, *Abies*, *Sequoia* and *Sequoiadendron*. Broadleaf genera are also well represented and include *Acer*, *Aesculus*, *Eucalyptus*, *Ilex*, *Magnolia*, *Nothofagus* and *Acacia*. The golf course has some woodland, much of which is unfragmented, forming a largely unbroken perimeter around that edge of the island. The woodland here is composed largely of deciduous trees, namely, oak, beech, sycamore, sweet chestnut and ash. Small patches of conifers (yew, Scots pine and Douglas fir) are also scattered among the woodland. For more detailed information on the tree



**Fig. 1** The 315 ha of Fota Island displaying the main recreational areas of the island and the areas of low, medium and high squirrel density

species present in the different areas see Haigh et al. 2015.

### Trapping

In February 2013, thirty cage traps, each with a nest box were placed around the island and pre-baited for a period of two weeks. Nine trapping sessions of four days each were carried out between March 2013 and March 2014. On the morning (dawn) of each trapping session, traps were baited with hazelnuts, whole maize and peanuts and were checked six hours later. Squirrel behaviour was recorded upon approach to a closed trap (Table 1). If vacant, traps were left pre-baited for the night.

Each trapped squirrel was flushed into a light hessian bag and the struggle rate (amount of time it moved around in the bag) of the individual was recorded for 30 s. The squirrel was then transferred into a wire-mesh 'handling cone' to minimise stress during handling and the breath rate was counted for 20 s. All animals were individually marked using passive integrated transponder tags (MID Fingerprint, Bournemouth, Dorset, UK) inserted into the nape of the neck. The sex and reproductive condition were recorded. An individual was considered to be in breeding condition if the nipples were visible in females and the testes were scrotal and large in males (Wauters and Dhondt 1993). Each animal was weighed using a Pesola spring scale balance with clip (NHBS, Devon, UK) and the shin length taken using vernier callipers. For an index of body condition (BCI) body mass was divided by shin length, a metric considered to be reflective of protein or fat reserves (or both) (Wirsing et al. 2002). As part of a larger study, faecal

samples were collected from the traps and used to examine variations in cortisol levels as an indicator of stress (Haigh et al. 2017). All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Licenses were obtained from the Department of Environment, Heritage and Local Government.

### Density

As part of a larger study, the density of squirrels in each area occupied by squirrels were calculated using the minimum number alive (MNA) (Haigh et al. 2015). This identified variations in density, allowing the classification of areas into high density ( $0.35 \pm 0.03$  per ha), medium density ( $0.17 \pm 0.03$ ) and low density ( $0.009 \pm 0.007$ ) (Fig. 1). Density was initially calculated using the whole area of the high density area, however, in reality the squirrels' distribution was concentrated in 8 of the 32 hectares that were not accessible to the public (Haigh et al. 2015). When this was taken into account a density of 3.25 squirrels per ha was observed in the high density area.

### Radio tracking

Ten individuals (5♀, 5♂) were fitted with PD-2C radio collars (Holohil Systems Ltd, Carp, Ontario, Canada). Two were collared in the low density area (1♀, 1♂) four in the high density area (3♀, 1♂) and four in the medium density area (1♀, 3♂). Maximum distance between traps was also measured for individuals to back up data in areas of low captures. Once collared, hourly fixes were

**Table 1** Ethogram of activities recorded on approaching trapped squirrels, and from the video footage of the open field test and mirror image stimulation test

Category	Approach	
	Behaviour	Description
	Moving in and out	Pacing between the nest box and trap
	Hiding	Stationary inside the nest box
	Peeping	In the nest box but looking out
	Escape	On the roof of the trap, trying to escape
	Feeding	Squirrel is engaged in eating some of the bait
<b>Open field test</b>		
Activity	Pacing	Squirrel constantly moving around the edge of the box and constantly moving
	Jumping	Squirrel is jumping against the lid of the box or onto the edge of the lid of the box
	Escape	Squirrel re-enters the handling tube from the box
Other	Stationary	Squirrel is not moving, and has its head tucked under and is not alert
	Defecate	Squirrel is defecating
	Groom	Squirrel is cleaning itself using its forelimbs
	Bipedal	Squirrel stands on its back legs with forelimbs raised and is looking from side to side
	Sniff	Squirrel is smelling the floor and walls of the box, its nostrils moving back and forth along the surface
<b>Mirror image stimulation test</b>		
Aggression	Bang	Squirrel is throwing itself against the mirror
	Hitting	Squirrel has approached the image and is hitting the image with its forelimbs
	Approach	Squirrel is moving towards the mirror with its head raised but does not touch the image or interact with it
Vigilance	Look	Squirrel is stationary but constantly looking from side to side
	Freeze	Squirrel remains in one spot and is immobile
	Tail	Squirrel is shaking its tail or hitting it against the ground
	Vocalisation	Squirrel is producing sounds (chattering, squealing, chuckling)

obtained for a period of 4–6 h, on 2 days a week over a 12 month period with each fix representing a sighting of the animal (Haigh et al. 2015). Behavioural tests (open field and mirror image stimulation tests) were conducted on all radio collared individuals.

### Behavioural tests

Behaviour related to activity in a novel environment was examined using an open field test (Boon et al. 2007) and aggression and sociability were measured using a mirror image stimulation test (Svendsen and Armitage, 1973). In the same manner as Boon et al. (2007, 2008), behavioural tests took place immediately after weighing and were conducted in a wooden open field box (60 × 80 × 50 cm) with a sliding perspex roof (ESM 1), as per the designs of Boon et al. (2007). The handling cone fitted into a hole at the side of the box and the squirrel backed into the box to enter. The trials were recorded through the Perspex roof using a digital video camera fitted on a tripod such that the whole field was in view (ESM 1). The camera was not visible to the squirrel during filming. A mirror was fitted to one end of the box but was covered during the open field test. Upon entrance into the box the squirrel's activity was filmed for seven and a half minutes (Boon et al. 2007).

After the open field test, the mirror was uncovered and the squirrel was filmed for a further 5 min. All tests were conducted at the site of capture and all tests were performed and scored by the same observer. It was not possible to record data blind because our study involved focal animals in the field.

### Behavioural analysis

Videos were scored using the J Watcher software (Blumstein et al. 2000). Before scoring began, a subsection of videos was examined and this was combined with observations in the field to develop an ethogram (Table 1). Behaviours were divided into those relating to movement and other activities for the open field test (Table 1) and behaviours related to aggression and vigilance for the mirror image stimulation test (Table 1). Footage from the open field test were analysed separately to the mirror image stimulation test. The time spent active as a percentage of total time of the open field test was then calculated for each individual. The time spent conducting other activities was also calculated for each individual.

For the mirror image stimulation test, data related to aggression and vigilance were measured, all other actions were ignored. The proportion of time spent being aggressive or vigilant was then calculated for each individual.

### Survival and recapture probability

Estimates of survival and recapture probabilities were calculated using capture and mark recapture estimates using live capture models in programme MARK (White and Burnham 1999). Comack-Joly Seber (CJS) models were used to examine the effects of area (high, medium and low density), sex (male and female) and time (Nine trapping sessions) on recapture and survival probabilities. The annual estimate of squirrel survival was cal-

culated from the product of the estimates of survival between each trapping session raised to the ninth power (nine sampling occasions in each year). Variation in time interval between capture sessions (4–8 weeks) was also accounted for. The saturated model was  $\phi$  (sex  $\times$  area  $\times$  time)  $p$  (sex  $\times$  area  $\times$  time), with  $\phi$  representing the survival probability between each trapping session and  $p$  denoting the probability of recapture at each 4 week trapping session. The goodness of fit was tested using the parametric bootstrap procedure to ensure that the saturated model adequately fit the data and did not violate the CJS assumptions i.e. ideally the  $\hat{c}$  value is close to 1 if the model assumptions are met (White and Burnham 1999). If the null hypothesis of  $\hat{c} = 1$  is rejected, the dataset is considered to display over-dispersion, however this can be corrected for if  $1 < \hat{c} < 3$ . If  $\hat{c}$  values  $> 3$ , it is assumed that the model does not adequately fit the data. The model deviance was simulated by running 1000 iterations and following this the  $\hat{c}$  was calculated by dividing the observed model deviance by the  $\bar{X}$  deviance of the simulated model.

In order to select the most parsimonious model, the saturated model was stepped down by first modelling the recapture probabilities while maintaining the saturated survival function ( $\phi$  sex  $\times$  area  $\times$  time). Following this survival ( $\phi$ ) was stepped down using the most parsimonious recapture function ( $p$ ). Models were selected based on the Akaike information criteria (AIC). A  $2 < \Delta AIC_c < 7$  shows that there is considerable support for a real difference in the adequacy of the models. If  $\Delta AIC_c < 2$  then the models have approximately equal weight in the data, in which case it is necessary to perform model averaging (Burnham and Anderson, 2002). The average value for a parameter is calculated by averaging over all models in the candidate model set with common elements in the parameter structure weighted by normalized AIC model weights (Cooch and White, 1999).

## Data analysis

Radio-fixes were plotted onto ArcMap (version 10.2) and the minimum convex polygons of home range were constructed on this software. All photographs of the site were also produced on ArcMap. SPSS statistics version 22 (IBM corp, NY) was used for all further statistical analysis.

A principal components analysis (PCA) was run for the open field test (OFT) and mirror image stimulation test (MIS) separately to reduce the number of behaviour variables (Boon et al. 2007). The suitability of PCA was assessed prior to analysis. In the open field test (OFT), escape, sniff and stationary were removed from the analysis as they failed to have at least one correlation where  $r = 0.3$  or above. The overall Kaiser-Meyer Oikin (KMO) measure was 0.6 and Bartlett's test of sphericity was statistically significant ( $P < 0.0005$ ). In the MIS test, the overall Kaiser-Meyer Oikin (KMO)

measure was 0.7 and Bartlett's test of sphericity was statistically significant ( $P < 0.0005$ ). Following the PCA, a linear mixed model (LMM) was conducted with the principal component scores as dependent variables, plus month of test, sex and area inhabited by the squirrel as fixed effects and squirrel identity (ID) as a random effect.

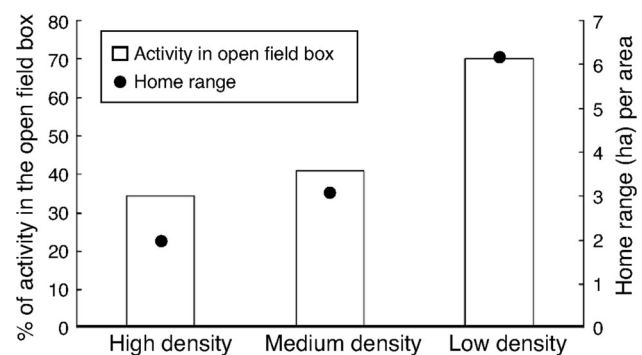
We tested for correlations among OF2 (Activity), MIS2 (Aggression), struggle rate and breathing rate using Pearson's product moment correlations in a pairwise manner among the four variables. False discovery rates were also calculated to account for multiple comparisons (Benjamini et al. 2001).

## Results

Fifty-six individuals (28♀, 28♂) were caught 141 times over the nine trapping sessions (March 2013–March 2014).

### Home range

During the study, a total of 1001 radio fixes were obtained (mean of  $99 \pm 0.70$  fixes per individual,  $n = 10$ ) over a mean of  $7 (\pm 0.17)$  months (range 4–12) for each individual. The radio collared squirrels were frequently trapped, being captured a mean of 7 times (range 3–11). Five squirrels first caught in the medium density area were occasionally seen in the high density area but those in the low density area were not seen outside of this zone. There was a significant variation in home range depending on population density (ANOVA:  $F_{2,9} = 6.071, P < 0.05$ ) and their activity (Fig. 2) in the open field box (ANOVA:  $F_{2,30} = 3.292, P < 0.05$ ) (Fig. 2). Radio tagged squirrels in the low density area had a greater home range ( $4.7 \pm 0.7$  ha), than those at high density ( $2.3 \pm 0.23$  ha).



**Fig. 2** The proportion (%) of time that radio tagged ( $n = 10$ ) squirrels from each area spent exploring in the open field box vs. their home range in the wild

## Approach, Struggle and breath rates

There was no consistence or significance in the action of the squirrels when the trap was approached and their activity ( $F_{4,68} = 1.252, P > 0.05$ ) in the open field box or aggression (ANOVA,  $F_{4,68} = 0.872, P > 0.05$ ) during the mirror image stimulation test. Therefore behaviour on approach was not deemed an indicator of how the squirrel would behave in the box and subsequently in the wild.

Variations were observed in the struggle and breath rates of squirrels inhabiting the different areas of the island. The mean struggle rates were higher in the low density, than in the medium or high density areas, where the lowest struggle rates were observed (Table 2). Breath rates were highest in the high density area (Table 2). However, this was not significant ( $P > 0.05$ ).

## Open field test-OFT

Sixty-nine behavioural tests were conducted on 32 individuals (15♀, 17♂). Seventeen individuals were tested more than once, with a mean of  $2 \pm 0.03$  (range 1–6) tests conducted on each individual. These squirrels came from all areas of the island (14-high density, 10 medium density, 8 low density). Squirrels varied considerably in the proportion of time that they spent engaged in activity in the open field box with some remaining stationary in the corner, while others spent the entire duration (7 ½ min) active, exploring all corners of the box and trying to escape through the roof or entrance.

The PCA revealed two components that had eigenvalues greater than one and which should be retained, they explained 47.1 and 23.9% of the total variance (Table 3). The two-component solution therefore explained 71% of the total variance. The first principal component (OF1) was characterised by grooming and being bipedal. The second (OF2) was characterised by movement (Jumping, pacing the box) and hereafter will be referred to as activity.

There was a significant effect of the density of the area both on the activity of the squirrels in the open field box ( $F_{3,68} = 3.242, P < 0.05$ ) and in the wild ( $F_{3,68} = 7.221, P < 0.05$ ). Squirrels in the low density area were more active in the open field box [mean ( $\pm$  SE) of  $54\% \pm 0.08$ ] and also moved further in the wild (furthest distance between traps captured-748.94 m), than those in the high density area who spent  $37\% \pm 0.09$  of their time engaged in explorative behaviour in the box and moved a maximum distance of

327.98 metres (Kruskall Wallis,  $P = 0.006$ -Tukey's post hoc test) in the wild.

## Mirror image stimulation test-MIS

Squirrels varied considerably in their response to their reflection (Table 1). Some squirrels turned their backs to the mirror or showed no response, while others threw themselves at the mirror and attacked the image with their forelimbs. Following the PCA, two components were retained from the MIS which explained 33.8 and 20.5% of the total variance (54.31% of the total variance) (Table 3). The first principal component (MIS1) was characterised by behaviours associated with anticipating danger (looking, freezing and hitting the tail at the back of the box (Table 3). These will be referred to as vigilance behaviour hereafter. The second component (MIS2) was characterised by attack and activities that took place at the front of the box and involves contact with the mirror (hit, approach and bang) (Table 3). These will be referred to as aggressive behaviours hereafter. There was a significant effect of area ( $F_{2,56} = 7.555, P = 0.002$ ) and month ( $F_{8,56} = 2.134, P = 0.05$ ) on the aggressiveness of squirrels but not of sex ( $F_{1,56} = 2.134, P = 0.091$ ) (Table 4). Squirrels in the low density areas spent a greater proportion of time being engaged in aggressive behaviour than those in the high density area (mean  $\pm$  SE- $11 \pm 0.5\%$  vs  $7 \pm 0.05$ ) or medium density area ( $6 \pm 0.14$ ).

## Activity and aggression

There were significant correlations between activity and aggressiveness ( $r = 0.44, df = 68, P < 0.01$ ) and aggressiveness and struggle rate ( $r = 0.38, df = 68, P < 0.05$ ). There was no correlation between aggressiveness and breathing rate ( $r = 0.08, df = 68, P = 0.68$ ), activity and breathing rate ( $r = 0.18, df = 69, P = 0.34$ ) or activity and struggle rate ( $r = 0.29, df = 68, P = 0.11$ ). None of these correlations was affected by the calculation of false discovery rates (Benjamini et al. 2001).

## Recapture and survival estimates

Squirrels in areas of high density had lower activity and showed a higher recapture rate than squirrels in the low

**Table 2** The mean ( $\pm$  SE) struggle and breath rates for all captures and squirrels where additional behavioural tests were conducted

Area	Mean ( $\pm$ SE) struggle rate (30 s) for all captures ( $n = 141$ )	Mean ( $\pm$ SE) breath rate per area (20 s) for all captures ( $n = 141$ )
High density	17.42 ( $\pm$ 0.03)	16.77 ( $\pm$ 0.03)
Medium density	18.9 ( $\pm$ 0.09)	15.52 ( $\pm$ 0.09)
Low density	20.6 ( $\pm$ 0.21)	14.95 ( $\pm$ 0.21)

**Table 3** PCA loadings for both an open field test (OFT) and mirror image stimulation test (MIS) performed on red squirrels

Behaviour	OFT1	OFT2	Behaviour	MIS1	MIS2
Jump	<b>-0.35</b>	<b>0.26</b>	Hit	<b>0.06</b>	<b>0.43</b>
Pace	0.16	<b>0.92</b>	Approach	-0.02	<b>0.45</b>
Bipedal	<b>0.54</b>	0.17	Bang	-0.24	<b>0.29</b>
Groom	<b>0.43</b>	0.11	Look	<b>0.43</b>	-0.05
			Freeze	<b>0.40</b>	0.01
			Tail	<b>-0.48</b>	<b>-0.47</b>
Stdev	1	1		1	1

Units are the percentage of time spent in each behaviour, unless indicated otherwise, and bold type indicates behaviours that contributed importantly to a component

**Table 4** Linear mixed model of levels of aggressive behaviour amongst red squirrels at different months of the year and from the low, medium and high density areas

	<i>df</i>	<i>F</i>	<i>P</i>
Intercept	1, 56	50.991	0.0001
Month	8, 56	3.449	0.003
Sex	1, 56	2.967	0.091
Area	3, 56	19.034	0.0001

density area. The top four models represented 55% of the model weight and so comprised what was considered to contain the best supported model set. For details on how the most parsimonious model was produced see *ESM 2*. The best model fit contained sex in the survival probability and sex and area in the recapture probability and there was evidence at the nominal  $\alpha = 0.05$  level of significant variation in recapture probabilities between the sexes and the three areas ( $\chi^2 = 12.043$ ,  $df = 5$ ,  $P = 0.034$ ) (Table 5). Despite variations in activity and aggression, no difference in survival was observed between the areas of different density (Table 6). This was also reflected in the fact that there was no significant difference in the BCI of squirrels occupying these different areas (Kruskall Wallis,  $P = 0.052$ ,  $P > 0.05$ ) (Fig. 3). Survival probability (sex) was contained in the top three models (Table 5). However, despite a lower

survival rate in females (Table 6), there was no significant difference (Mann-Whitney,  $P = 0.974$ ,  $P > 0.05$ ) in the BCI of males and females (males ( $n = 28$ ) BCI of  $5.4 \pm 0.42$  ( $\pm$ stdev) and females ( $n = 28$ ) BCI of  $5.4 \pm 0.45$ ).

#### Breeding condition

Density did not significantly influence breeding condition ( $F_{2,140} = 1.202$ ,  $P > 0.05$ ). Males and females both showed peaks in breeding condition in June (86% ♀, 100% ♂) (Fig. 4). There was a significant difference in the number of males and females caught in breeding condition ( $F_{27,27} = 6.876$ ,  $P < 0.05$ ) and while a proportion (range 10–100%) of captured males were in breeding condition in all months of the year, females were not, and instead showed peaks in June (86%) and a second peak in October (67%) (Fig. 4).

#### Discussion

A key element of animal personalities is the potential correlation among behavioural traits (Minderman et al. 2009). In the current study, there was a significant correlation between an individual's aggressiveness,

**Table 5** Comack- Joly Seber models showing the most parsimonious models

	Model	AIC	$\Delta$ AIC	AIC weight	No. Par.	Deviance	LRT
<b>1</b>	<b><math>\Phi</math> (sex) P (sex*area.)</b>	<b>276.8578</b>	<b>0.0000</b>	<b>0.20328</b>	<b>8</b>	<b>167.8236</b>	
2	$\Phi$ (sex) p (.)	277.6511	0.7933	0.13672	3	179.8662	Models 1 and 2: $P = 0.03$
3	$\Phi$ (sex*area) p (.)	278.1326	1.2748	0.10747	7	171.4401	
4	$\Phi$ (.) p (sex*area)	278.1351	1.2773	0.10733	7	171.4426	Models 1 and 3: $P = 0.06$
5	$\Phi$ (.) p (.)	279.0142	2.1564	0.06916	2	183.3481	Models 2 and 3: $P = 0.08$
6	$\Phi$ (area) p (sex*area)	279.2222	2.3644	0.06233	9	167.7975	
7	$\Phi$ (sex) p (sex)	279.6174	2.7596	0.05115	4	179.6717	
8	$\Phi$ (.) p (sex)	279.8009	2.9431	0.04667	3	182.0160	
9	$\Phi$ (area) p (.)	280.1110	3.2532	0.03996	5	177.9614	
10	$\Phi$ (sex*area) p (sex)	280.2682	3.4104	0.03694	8	171.2341	
	Saturated model $\Phi$ (sex*area*time) p (sex *area* time)	498.8891	222.0313	0.0000	62	101.6651	

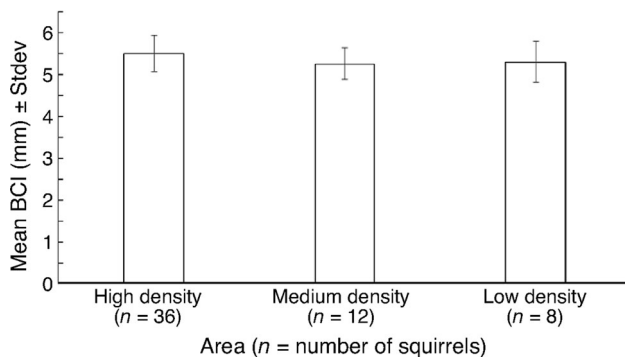
The model used for parameter estimation is represented in bold

$\phi$  survival probability,  $p$  recapture probability, *No. Par* number of parameters, *LRT* likelihood ratio tests

**Table 6** Parameter estimates for  $\phi$  (survival) and  $p$  (recapture), calculated from the most parsimonious model ( $\phi$  (sex)  $p$  (sex\*area)) using model averaged values

Between trapping sessions (4 weeks)	Annual (36 weeks)-9 trapping sessions
Survival estimate ( $\pm$ SE)	
♂ 0.918 ( $\pm$ 0.031)	♂ 0.46
♀ 0.805 ( $\pm$ 0.053)	♀ 0.14
Recapture estimate ( $\pm$ SE)	
FH 0.42 ( $\pm$ 0.09)	FH 0.000407
FM 0.40 ( $\pm$ 0.11)	FM 0.000262
FL 0.25 ( $\pm$ 0.22)	FL 0.000004
MH 0.48 ( $\pm$ 0.08)	MH 0.001353
MM 0.43 ( $\pm$ 0.09)	MM 0.000503
ML 0.31 ( $\pm$ 0.20)	ML 0.000026

F female, H high density ♀, FM medium density ♀, FL low density ♀, M male, H high density ♂, MM medium density ♂, ML low density ♂



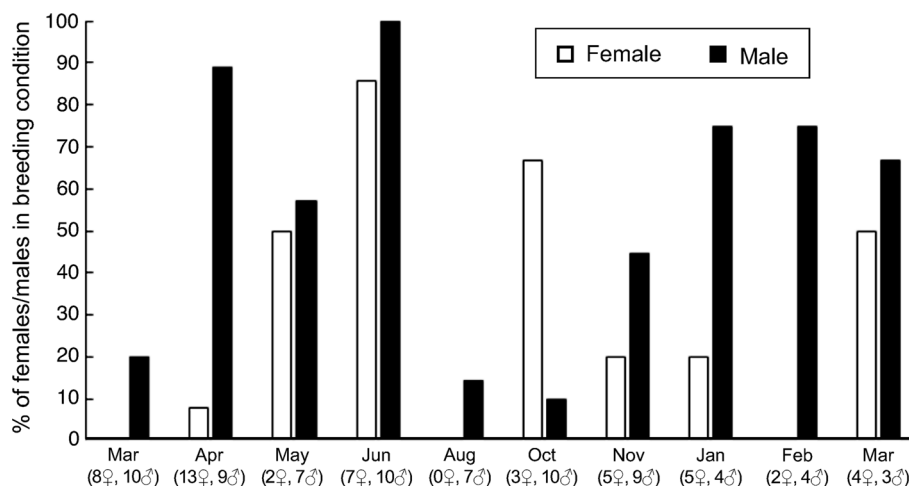
**Fig. 3** The mean body condition index (BCI = weight (g)/shin length (mm))  $\pm$  stdev of squirrels in the low, medium and high density areas of the island

activity and struggle rate, with more aggressive individuals moving more, both in the open field box and in the wild. These individuals were also consistent with

Boon et al.'s. (2007) study, in that they struggled the most during the handling test. However, aggressiveness or activity was not significantly correlated with breath rate and in contrast to Boon et al.'s. (2007) study, they had a lower breathing rate than less aggressive individuals. Despite extensive trapping in the low density area (540 trap days) only eight squirrels were available for behavioural testing, therefore it is unclear whether this pattern would be still apparent if more individuals had been tested, or whether they would have shown a similar pattern to that of Boon et al. (2007).

As well as being less aggressive and active and occurring at a higher density, squirrels in high density areas also had higher faecal cortisol metabolites than squirrels in other areas of the island, with squirrels in low density areas having the lowest levels (Haigh et al. 2017). The fact that these squirrels also had the lowest faecal cortisol metabolite levels may account for this lower breath rate. Carere and van Oers (2004) found that the breath rate was higher in shy than in bold great tits and that breath rates are indicators of acute stress in songbirds. Physiological components of stress include increased respiration rate, which shift metabolism toward energy mobilisation and away from energy conservation (Morgan and Tromborg, 2007).

As part of a larger study genetic samples were taken from all captured squirrels ( $n = 56$ ) and that of squirrels on the nearest woodland from the island (1.5 km) and they were not found to be genetically similar. Furthermore, the island population were shown to have little genetic variability and high levels of inbreeding (Haigh et al. unpublished data). It would therefore appear that dispersal off the island was not a common phenomenon and instead dispersal may have involved movement to other areas of the island. In Wauters et al. (2011) study the mean dispersal distance ( $\pm$ SD) was  $1014 \pm 925$  metres, with, 50% of the immature red squirrels dispersing more than 320 metres but less than 1500 metres away from the natal site (Wauters et al. 2011). Similarly, Wauters et al. (1994) observed that



**Fig. 4** The percentage of times captured male and female squirrels were in breeding condition per month



most young squirrels disperse within 1 km in fragmented landscapes. Squirrels in the low density area were more aggressive and explorative in the open field box, but also had a larger home range and higher struggle rate than squirrels in the high density area. In several taxa, comparisons between dispersers and residents have revealed differences in activity patterns, aggressiveness, social behaviour and mating decisions (Cote et al. 2010). The dispersal process itself might select for bold-aggressive individuals (i.e. only they disperse), which then have a particularly strong tendency to disrupt invaded communities (Sih et al. 2004). Bekoff (1977) predicted that individuals who socialised with or are not repulsed by others were less likely to disperse, which could account for the high density of squirrels observed in the food optimum area (Haigh et al. 2015). In contrast, it would appear that the low density area does not represent optimum habitat and is made up of dispersing individuals something which is indicated further by the lower recapture rates of squirrels in this area and longer distances travelled. Hoset et al. (2011) observed that in root voles, *Microtus oeconomus*, dispersers were, on average, faster explorers and were more active than residents. As well as exploring more widely in the box and in the wild, individuals in the low density area were more aggressive, indicating that squirrels on the island may inhabit areas depending on their propensity to be social with conspecifics. Ims (1990) reported a positive correlation between dispersal distance and avoidance behaviour in female grey-sided voles, *Myodes rufocanus* and during peaks of population densities meadow vole *Microtus pennsylvanicus* males that dispersed were more aggressive than others (Myers and Krebs 1971).

Human induced changes, such as climate change (Bradshaw and Holzapfel 2006), the spread of urbanization (Parker and Nilon 2012; Jokimäki et al. 2017) and habitat fragmentation (Verboom and Van Apeldoorn 1990), has forced individuals to either adapt to these changes or disperse, and such changes may be more detrimental to individuals displaying certain traits. Therefore, depending on temperament, individuals within a population may vary in their potential to occupy areas with different levels of disturbance. In the current study, the less aggressive, less active squirrels inhabited an area that while containing optimum food resources (Haigh et al. 2015), was subject to much human disturbance with the wildlife park receiving over 300,000 visitors a year. While Parker and Nilon's (2008) observed grey squirrels at higher densities to be more aggressive, the opposite was found in the current study. Unaggressive, shy (reactive) individuals have been shown to display more flexible behaviour (Koolhaas et al. 1999), and may therefore demonstrate a greater tolerance to conspecifics. Sih et al. (2004) observed how proactive individuals are both aggressive and bold and while they tend to dominate and out-compete reactive ones in a stable environment, reactive individuals appear to respond better to changing environments (Sih et al.

2004). Koolhaas et al. (1999), commented how reactive (i.e. docile, and non-explorative) animals show higher cortisol release, in response to a stress, than do proactive individuals (i.e. active, non-docile, and highly explorative). The fact that squirrels in the high density area, despite being more docile and occurring at a high density, still displayed the highest levels of faecal cortisol metabolites, demonstrates that this high density living, coupled with a need to suppress aggression for survival, resulted in a considerable accumulation of stress. Behaviourally, chronic stress may be indicated by reduced exploratory behaviour and increased behavioural inhibition (Carlstead et al. 1993; Carlstead and Brown 2005), as was observed amongst the squirrels in the current study. However, this was found to have no effect on survival rates.

In the current study squirrels were not distributed evenly throughout the island but clustered their activity along a network of yews running from the medium to high density area (Haigh et al. 2015). Despite a higher density and subsequent potential greater competition for resources in the high density area, these squirrels explored less and had smaller home ranges than squirrels in the low density area, where yew trees were sparsely distributed and squirrels moved further and appeared at lower densities. This variation in resources may have influenced behaviour as Nicolaus et al. (2012) observed that in wild great tits (*Parus major*) individuals with experimentally decreased survival probability became faster explorers (i.e. increased risk-taking behaviour) compared to individuals with increased survival probability. These individuals who have greater resources and conversely higher future fitness expectations would behave cautiously to reduce mortality risks (e.g. agonistic interactions with conspecifics) which in return would reinforce their future assets (Nicolaus et al. 2012). As there was no difference in survival rates, body condition and breeding activity between the different areas in the current study, it would suggest that these squirrels, occurring in areas of lower resources and at lower population density can successfully achieve comparable energy budgets, through increasing their activity.

In the current study females had a lower survival rate than males. While animals are expected to optimize their lifetime reproductive success, the energy expended during reproduction likely leads to an increased risk of mortality (Saino et al. 1999). In polygynous or promiscuous mammals, male mating effort can have significant costs due to the risks associated with dispersal (Hoffman et al. 2008). In Columbian ground squirrels with seasonal reproduction, male mortality is generally high during or after the mating season, whereas female mortality is high in conjunction with the birth season and lactation (Neuhaus and Pelletier, 2001). In stable habitats and if the home range contains a stable food supply (Lurz et al. 2000) resident adult red squirrels generally remain within the first home range

that they establish throughout their lives (Wauters and Dhondt 1992). Lurz et al. (2000) observed that in these stable, high-density populations territory shifts are rare and occur only when a nearby vacant territory containing more food than the old one is available. Similarly, in the current study squirrels were not recorded to disperse off the island as evidenced by high recapture rates, therefore the mortality rates associated with male dispersal may not be apparent. Therefore, the fitness consequences of reproduction may be more apparent amongst females leading to a corresponding reduction in their survival.

## Conclusion

In conclusion, as well as showing variations in density and faecal cortisol metabolites, squirrels on the island showed variation in their activity and aggression depending on whether they inhabited the high or low density area. However, there was no corresponding effect on the survival probability, body condition or breeding condition amongst these individuals. The squirrels in the low density area were more aggressive and active and it is suggested that the squirrels in this area may have been made up of dispersing individuals, as the dispersal process itself might select for bold-aggressive individuals (Sih et al. 2004). In contrast, the high density area which was also subject to the greatest human disturbance, consisted of less aggressive, less explorative individuals which may have been better suited to this changing environment.

**Acknowledgements** This work was supported by The Irish Research Council, Enterprise Partnership Scheme and Fota Wildlife Park. The authors would like to extend a special thank you to Simon O'Hara of The Fota Resort, Sean McKeown and all the staff of Fota Wildlife Park and gardens and Emily Goldstein of University College Cork. The authors would also like to extend their gratitude to the anonymous reviewers, for their constructive comments, and improvements which they made to the manuscript.

## Compliance with ethical standards

**Funding** The study was funded by The Irish Research Council, Enterprise Partnership Scheme and Fota Wildlife Park Postdoctoral Fellowship (EPSPD/2012/313).

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethical approval** All procedures performed involving animals were in accordance with the ethical standards of the institution at which the studies were conducted and with national guidelines.

**Informed consent** Consent to submit has been received explicitly from all co-authors, as well as from Fota Wildlife Park where the work has been carried out.

**Data availability** The datasets produced and analysed during the current study are available from the corresponding author on reasonable request.

## References

- Adriaenssens B, Johnsson JI (2011) Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. *Behav Ecol* 22:135–143
- Andren H, Delin A (1994) Habitat selection in the Eurasian red squirrel, *Sciurus vulgaris*, in relation to forest fragmentation. *Oikos* 70(1):43–48
- Bekoff M (1977) Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *Am Nat* 715–732
- Benjamini Y, Drai D, Elmer G, Kafkafi N, Golani I (2001) Controlling the false discovery rate in behavior genetics research. *Behav Brain Res* 125:279–284
- Betts BJ (1976) Behaviour in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. *Anim Behav* 24(3):652–680
- Blumstein DT, Evans CS, Daniel JC (2000) JWatcher TM 0.9 An Introductory User's Guide
- Boon AK, Reale D, Boutin S (2007) The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol Lett* 10:1094–1104
- Boon AK, Reale D, Boutin S (2008) Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* 117:1321–1328
- Boonstra R, Lane JE, Boutin S, Bradley A, Desantis L, Newman AE, Soma KK (2008) Plasma DHEA levels in wild, territorial red squirrels: seasonal variation and effect of ACTH. *Gen comp endocrin* 158(1):61–67
- Both C, Dingemanse NJ, Drent PJ, Tlinbergen JM (2005) Pairs of extreme avian personalities have highest reproductive success. *J Anim Ecol* 74:667–674
- Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science (Washington)* 312(5779):1477–1478
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, Springer Science and Business Media
- Carere C, Van Oers K (2004) Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. *Physiol Behav* 82:905–912
- Carlstead K, Brown JL (2005) Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. *Zoo Biol* 24:215–232
- Carlstead K, Brown JL, Strawn W (1993) Behavioral and physiological correlates of stress in laboratory cats. *Appl Anim Behav Sci* 38:143–158
- Coch E, White G (1999) MARK: an introductory guide
- Cote J, Dreiss A, Clobert J (2008) Social personality trait and fitness. *Proc R Soc B: Biol Sci* 275:2851–2858
- Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Phil Trans R Soc B: Biol Sci* 365:4065–4076
- Haigh A, O'Riordan R, Butler F (2015) The preference for yew (*Taxus baccata*) by a red (*Sciurus vulgaris*) only squirrel population. *Wildl Res* 42(5):426–436
- Haigh A, Butler F, O'Riordan R, Palme R (2017) Managed parks as a refuge for the threatened red squirrel (*Sciurus vulgaris*) in light of human disturbance. *Biol Conserv* 211:29–36
- Hoffman CL, Ruiz-Lambides AV, Davila E, Maldonado E, Gerald MS, Maestripieri D (2008) Sex differences in survival costs of reproduction in a promiscuous primate. *Behav Ecol Sociobiol* 62:1711–1718
- Hoset KS, Ferchaud AL, Dufour F, Mersch D, Cote J, Le Galliard JF (2011) Natal dispersal correlates with behavioral traits that are not consistent across early life stages. *Behav Ecol* 22:176–183
- Ims RA (1990) Determinants of natal dispersal and space use in grey-sided voles, *Clethrionomys rufocanus*: a combined field and laboratory experiment. *Oikos* 106–113

- Jokimäki J, Selonen V, Lehikoinen A, Kaisanlahti-Jokimäki ML (2017) The role of urban habitats in the abundance of red squirrels (*Sciurus vulgaris*, L.) in Finland. *Urban For Urban Gree*
- Koolhaas J, Korte S, De Boer S, Van Der Vegt B, Van Reenen C, Hopster H, De Jong I, Ruis M, Blokhuis H (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci Biobehav Rev* 23:925–935
- Korpela K, Sundell J, Ylonen H (2011) Does personality in small rodents vary depending on population density? *Oecol* 165:67–77
- Lurz PW, Garson P, Wauters LA (2000) Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). *J Zool* 251:167–178
- Minderman J, Reid JM, Evans PG, Whittingham MJ (2009) Personality traits in wild starlings: exploration behavior and environmental sensitivity. *Behav Ecol*. doi:10.1093/beheco/arp067
- Møller AP (2010) Interspecific variation in fear responses predicts urbanization in birds. *Behav Ecol* 21:365–371
- Morgan KN, Tromborg CT (2007) Sources of stress in captivity. *Appl Anim Behav Sci* 102:262–302
- Myers JH, Krebs CJ (1971) Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecol Monograph* 53–78
- Neuhaus P, Pelletier N (2001) Mortality in relation to season, age, sex, and reproduction in Columbian ground squirrels (*Spermophilus columbianus*). *Can J Zool* 79:465–470
- Nicolaus M, Tinbergen JM, Bouwman KM, Michler SP, Ubels R, Both C, Kempnaers B, Dingemans NJ (2012) Experimental evidence for adaptive personalities in a wild passerine bird. *Proc R Soc Lond B Biol Sci* 279(1749):4885–4892
- Parker TS, Nilon CH (2008) Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosyst* 11(3):243–255
- Parker TS, Nilon CH (2012) Urban landscape characteristics correlated with the synurbanization of wildlife. *Landsc Urban Plan* 106(4):316–325
- Penke L, Denissen JJ, Miller GF (2007) The evolutionary genetics of personality. *Eur J Pers* 21:549–587
- Promislow DE (1992) Costs of sexual selection in natural populations of mammals. *Proc R Soc Lond Series B: Biol Sci* 247:203–210
- Reale D, Gallant BY, Leblanc M, Festa-Bianchet M (2000) Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim Behav* 60:589–597
- Saino N, Calza S, Ninni P, Møller AP (1999) Barn swallows trade survival against offspring condition and immunocompetence. *J Anim Ecol* 68:999–1009
- Selonen V, Hanski IK (2010) Condition-dependent, phenotype-dependent and genetic-dependent factors in the natal dispersal of a solitary rodent. *J Anim Ecol* 79(5):1093–1100
- Selonen V, Hanski IK, Mäkeläinen S (2012) Predictors of long-distance dispersal in the Siberian flying squirrel. *Evol Ecol* 26(6):1361–1369
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evolut* 19:372–378
- Svendsen G, Armitage K (1973) Mirror-Image Stimulation Applied to Field Behavioral Studies. *Ecology* 54:623–627
- Verboom B, Van Apeldoorn R (1990) Effects of habitat fragmentation on the red squirrel. *Sciurus vulgaris* L *Landsc Ecol* 4(2–3):171–176
- Wauters L, Dhondt AA (1989) Body weight, longevity and reproductive success in red squirrels (*Sciurus vulgaris*). *J Anim Ecol* 637–651
- Wauters L, Dhondt AA (1992) Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. *Anim Behav* 43:297–311
- Wauters L, Dhondt AA (1993) Immigration pattern and success in red squirrels. *Behav Ecol Sociobiol* 33:159–167
- Wauters LA, Lens L (1995) Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. *Ecology* 2460–2469
- Wauters LA, Hutchinson Y, Parkin DT, Dhondt AA (1994) The effects of habitat fragmentation on demography and on the loss of genetic variation in the red squirrel. *Proc R Soc London B: (Bio)* 255(1343):107–111
- Wauters LA, Preatoni D, Martinoli A, Verbeylen G, Matthysen E (2011) No sex bias in natal dispersal of Eurasian red squirrels. *Mammal Bio-Zeitschrift für Säugetierkunde* 76(3):369–372
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139
- Wirsing AJ, Steury TD, Murray DL (2002) Relationship between body condition and vulnerability to predation in red squirrels and snowshoe hares. *J Mammal* 83:707–715