



Helpers but not breeders adjust provisioning effort to year-round territory resource availability in carrion crows

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In most cooperatively breeding bird species, individuals live year round in all-purpose territories that may vary greatly in quality. Territory resource availability is likely to influence the investment in provisioning the brood, and different group members may respond in different ways, according to individual strategies of investment in self-maintenance or current reproduction. Although this may be important for understanding division of labour within the group, few studies have investigated how individuals respond to changing conditions 'at home'. In cooperatively breeding carrion crows, *Corvus corone*, chick provisioning is costly and both breeders and helpers allocate additional resources to self-maintenance, rather than the current brood, when food availability is temporarily augmented during the breeding season. However, here we show that helpers, but not breeders, increased their chick-feeding rate when territory resources were experimentally enhanced throughout the year. These results indicate a role of year-round territory quality in shaping cooperation at the nest in this species. We suggest that the probabilities of reproducing in the following breeding season, which are higher for breeders than for helpers, modulate the effect of long-term resource abundance on individual provisioning decisions, leading to a higher investment in the current brood by helpers only.

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The factors determining individual provisioning decisions in cooperative species are important for investigating the evolution of cooperative behaviour, but they are not yet fully understood (Koenig & Dickinson 2004). Typically, factors such as breeding status, sex, age and relatedness to the chicks are considered potentially important predictors of individual effort, but little attention has been paid to the costs of provisioning (Cockburn 1998), and how they change with resource availability. If chick provisioning entails costs, individual allocation of resources will depend

on the trade-off between current reproduction (feeding current young) and future reproduction (maintaining body condition or future fecundity; Kacelnik & Cuthill 1990; Markman et al. 2002). This trade-off is likely to be crucial in determining the individual contribution to chick rearing in cooperatively breeding species, which are typically long lived (Covas & Griesser 2007) and are therefore expected to rate the 'future' highly and to fine-tune current effort. In addition, because different group members usually differ in their reproductive value according to their sex, age and social status, the trade-off between current and future reproduction will vary among individuals, ultimately affecting the distribution of labour within the group.

In biparental bird species, energy allocation may depend on environmental conditions: self-maintenance is preferred when resources are scarce or unpredictable, whereas investment in the current brood increases when food is abundant and the parents are in good condition (Weimerskirch et al. 2001; Velando & Alonso-Alvarez 2003). This

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approach has proved useful in understanding provisioning decisions in many avian species and is potentially important in explaining individual contribution in cooperative societies because (1) cooperatively breeding populations typically live in year-round all-purpose territories (Brown 1987) that may vary greatly in quality (Stacey & Ligon 1991; Komdeur 1992; Baglione et al. 2005) and (2) different group members are likely to respond to resource availability in different ways, according to individual strategies of investment in self-maintenance or current reproduction. However, only a few studies have addressed resource allocation in response to variable costs of provisioning in cooperative species. In meerkats, *Suricata suricatta* (Clutton-Brock et al. 2002), white-winged choughs, *Corcorax melanorhamphos* (Boland et al. 1997) and moorhens, *Gallinula chloropus* (Eden 1987) helpers increased their feeding effort when food was supplemented during the breeding period. The response of breeders was similar to that of helpers in white-winged choughs, while moorhen adults lowered chick-feeding rates in food-supplemented territories. In cooperative carrion crows, *Corvus corone*, conversely, both breeders and helpers responded to a reduction in the immediate costs of provisioning (food supplementation during the breeding season) by investing in self-maintenance, that is by maintaining their weight rather than increasing provisioning rates, showing that the 'future' is generally important for individuals (Canestrari et al. 2007).

Most cooperatively breeding birds, however, are territorial year round (Arnold & Owens 1999) and may be sensitive to conditions in their territory throughout the year. If self-maintenance constrains investment in current reproduction, individual strategies may change beyond a threshold of resource availability. In particular, given high costs of provisioning, individuals might increase provisioning rates when food is abundant and predictable over the long term because the negative consequences for their own survival will be more easily reduced. This may be especially important for understanding individual contributions to chick care in cooperatively breeding carrion crows, where territories vary greatly in quality (Baglione et al. 2005) and where group members have different prospects for future reproduction (D. Canestrari, unpublished data), which are likely to affect their response to changing resource conditions. In this study, we tested in this species whether year-round food abundance influences individual provisioning decisions, and whether individual strategies vary according to breeding status (breeder versus helper) and sex. To do so, we compared provisioning patterns of male and female breeders and helpers in territories that were food supplemented year round with those of control groups that were kept unfed. Using the results of both this study and previous experiments, we discuss the role of territory quality in shaping cooperation at the nest in carrion crows.

METHODS

Study Area and Population

Since 1995, we have studied a population of carrion crows in a 45 km² rural area in northern Spain (42°N, 5°W).

The study area represents a traditional Spanish low-intensity agricultural landscape, with a mosaic of crops, meadows, poplar and pine plantations, scrub, patches of oak forest and uncultivated land. In this population, carrion crows form cohesive groups of up to nine individuals through both delayed dispersal of offspring, which can remain on their natal territory with their parents for up to 4 years, and/or immigration of individuals that are related to the resident breeder of the same sex (Baglione et al. 2002a, 2003). Sex ratio in the groups is skewed towards males, but females are found among both nondispersing offspring and immigrants. Unlike nondispersing offspring, adult immigrants (mainly males, but occasionally females too) can share reproduction with the dominant pair (Baglione et al. 2002b) and both nondispersing offspring and immigrants can participate in nestling care.

Breeding females lay one to six eggs per breeding attempt. If nests fail at the egg or hatching stage, females may renege up to three times, but a maximum of one successful brood is raised per year. Although helpers feed the nestlings at a lower rate than breeders (Canestrari et al. 2005), their contribution to care enhances the annual production of fledglings (Canestrari et al. 2008). Provisioning the chicks leads to members of all categories losing an average of 5.4% of initial weight and this weight loss is proportional to provisioning effort (Canestrari et al. 2007). However, helpers lighten the workload of breeders, who reduce their provisioning effort when assisted by more than one additional caregiver (Canestrari et al. 2007).

Bird Banding and Radiotracking

Each year since 1999 we have captured crows using two-compartment walk-in traps and a remote-controlled snap trap (3 × 3 m) specifically developed for this species, which allowed us to catch two to five individuals at one time (Baglione et al. 2002a). No crows were injured or abandoned the nest or territory as a consequence of capture. The individuals were marked with a unique combination of colour rings and plastic patagial wing tags (6.5 × 3.5 cm, custom made) that did not affect survivorship (Caffrey 2000; Canestrari et al. 2007). The birds were aged as 1, 2, and older than 2 years according to the internal colour of the upper mandible (Svensson 1992). The nestlings were banded just before they left the nest (30 days after the first chick in the brood hatched) and those born in 2003 and 2004, when this experiment was carried out, were fitted with a radiotransmitter (Holohil RI-2B, Holohil System Ltd., Carp, Ontario, Canada) attached with a leg harness made of 3 mm silicon string (Baglione et al. 2006). This allowed us to follow the movements of juveniles to and from the territories. In a previous study, we found that there is not a clear dichotomy in the dispersal strategy of young crows (dispersing versus remaining at home). Rather, juveniles show a gradient of philopatry, varying greatly in their allocation of time spent at home versus time spent roaming outside the natal territory throughout the year. Furthermore, year-round food supplementation increases philopatry significantly (Baglione et al. 2006). This may in turn affect feeding

effort, because juveniles that visit the natal territory only occasionally have less time for helping at the family nest. To circumvent this problem, we restricted our sample to juveniles that spent more than 70% of the time in the natal territory throughout the year ('philopatric offspring' hereafter). This proportion of time was assessed from radiotracking data (three localizations a week for the whole first year of life; see [Baglione et al. 2006](#) for details). Fed and unfed philopatric juveniles included in our sample did not differ significantly in their proportion of time spent on the natal territory during the breeding season (restricted maximum likelihood test, including sex as an additional explanatory variable and territory as a random term: $\text{Wald}/df = 0.05$, $df = 1$, $P = 0.82$), and therefore had the same opportunities to contribute to chick provisioning.

Radiotransmitters weighed 11 g, which corresponded to 3.3 and 2% of the body weight of the lightest and the heaviest fledglings, respectively. On average, they weighed 2.6% of fledgling mass. For six of 100 banded fledglings, the radiotransmitter weighed slightly more than 3% of their body weight, but all these juveniles were the youngest in their brood and had not yet reached their final fledging weight. Radiotransmitters did not seem to affect juvenile survival during the first year, when mortality rate is highest. The proportion of radiotagged yearlings that survived did not differ significantly from that of yearlings banded between 1995 and 2003 without radiotransmitters (average annual percentage of resighted radioequipped juveniles: 36.7%, range 33.3–39.3%; average annual percentage of resighted nonradioequipped juveniles: 38.7%, range 22.4–50.9%, Yates-corrected $\chi^2_1 = 0.08$, $P = 0.78$). Radiotransmitter batteries lasted about 18 months. Nineteen juveniles that were recaptured about 12 months after fledging (eight of them were recaptured a second time within the following 3 months) showed no signs of skin irritation or infection from the presence of the radio, which was not removed because it was still working. In only one case was the radiotransmitter removed because, owing to displacement, the tube was rubbing the skin. No other individuals showed apparent signs of distress or difficulties in walking or flying. Since 2004, expired radios have been removed, if they had not already been lost, when individuals were recaptured. We collected between 50 and 200 μl of blood from the brachial vein of each banded individual for molecular sexing ([Griffiths et al. 1998](#)). All bird manipulations were authorized by Junta de Castilla y León.

Food Supplementation Experiment

In crow groups where several individuals can potentially breed, unsuccessful breeders (i.e. adults that mated within their group but failed to produce offspring) cannot be told apart from truly nonbreeding helpers. To avoid this problem, for this study we chose groups containing individuals whose status could be assigned unambiguously (see below). At the end of the breeding seasons in 2003 and 2004, we paired groups of similar size, and randomly assigned one group of each pair to the experimental

treatment (43 groups in total). We fed the experimental groups with 400 g of canned dog food and 200 g of maize per group member three times a week in the middle of the territory (about 200 m away from the nest) until the end of the following breeding season (i.e. until the chicks fledged or the nest failed at the egg or nestling stage). The dog food used (brand DIA, flavour chicken and beef) falls within the natural range of variability of the crow's diet in terms of proportions of animal and vegetable components, and the individual daily amount of food supplemented was calculated to cover the daily energetic requirements of all group members, approximately 818.5 kJ/crow per day ([Nagy et al. 1999](#); [Baglione et al. 2006](#)), without exceeding the range of natural variation of food resources in crow territories. Details of the calculation of this range are given in [Canestrari et al. \(2007\)](#). Briefly, based on the daily expenditure of group members, food availability was estimated to vary by up to 6164.8 kJ/day between territories. The experimental food supplementation provided on average 3070.4 kJ/day per territory. This suggests that the experimental treatment was unlikely to create unnatural conditions for the crows. After a few days of treatment, the experimental crows habituated to the food supplementation. Video-recording sessions in all experimental groups confirmed that the target crows were actually taking the food and that no group member was prevented from access. Typically, the supplementary food was removed and eaten or stored within 20 min of our departure.

During the breeding seasons in 2004 and 2005, we videorecorded activity at the nests by placing camouflaged video cameras 2.5 m away from the nests. The birds never showed any visible reaction to the video cameras and videorecorded nests did not show a higher rate of brood failure than control nests without video cameras ([Canestrari et al. 2005](#)). For each nest we collected three to five recording bouts of 4 h each, between day 10 and day 15 from hatching. We measured individual provisioning rate as the number of feedings/h, where 'feeding' is defined as every act of delivering food to a chick's open gape. We have shown previously that the number of feedings per visit to the nest is correlated with the amount of food carried by a crow in its crop ([Canestrari et al. 2005](#)). Eventually we collected information on seven fed groups and 14 unfed groups, because, owing to early nest failures or inaccessibility of nests for recording, not all the initial study groups could be sampled. Although this disrupted our original matching of control and experimental territories according to group size (see above), the final sample was still balanced, with no significant difference in group size between fed and unfed territories (fed groups: $\bar{X} \pm \text{SE} = 4.57 \pm 0.49$; unfed groups: 4.29 ± 0.28 ; Student's t test: $t_{19} = 0.38$, $P = 0.7$). Each group was sampled only once. Eighteen groups comprised a breeding pair and one to three yearling nondispersing offspring. Of these, four included only banded individuals. In the other 11 groups, all except one member (a breeder) were banded. Here, the sex of the unbanded breeder was inferred from the composition of the rest of the group ([Canestrari et al. 2007](#)). Because only one of 44 breeders studied so far in this population was younger than 3 years (D. Canestrari, unpublished data), these

unbanded breeders were aged as adults. In the remaining three groups where both parents were unbanded, only data from yearling nondispersing offspring were considered. In the other three groups, which contained one banded breeder, one or two unbanded immigrants and one to three yearling nondispersing offspring, only banded individuals were considered. In this sample, all helpers were 1-year-old nondispersing offspring and are called 'helpers' hereafter. Overall, we obtained information on 13 breeders and 10 helpers in the seven fed groups, and 20 breeders and 20 helpers in the 14 unfed groups.

In 2004, this experiment overlapped with that described in Canestrari et al. 2007 (see Introduction) which was carried out in 2003 and 2004 and focused on the effects of short-term food supplementation (breeding season) on provisioning effort. In 2004, nine control territories (unfed) were shared between the two experiments.

Weight Measurements

Members of experimental and control groups were weighed a few days (1–3) before egg hatching by using an 'Ohaus Champ II' digital precision bench scale (capacity \times readability: 15×0.002 kg) with a separate display. The scale was camouflaged and measures were taken with a system of two video cameras, one pointing at the scale and the other at the display. The crows were attracted to the scale with bait (one chicken carcass tied to the top of the scale; for further details see Canestrari et al. 2007). We weighed 26 breeders (19 males and 7 females) and 25 helpers (18 males and 7 females). At the end of the nestling period, we also tried to weigh those crows that successfully raised young, to calculate their mass loss in relation to their provisioning effort. However, in this second round, we could obtain information on only five fed individuals, which were insufficient for a comparison with unfed crows.

Statistical Analyses

For statistical analyses we used Genstat 6.1 (VSN International Ltd., Hemel Hempstead, U.K.). All data were analysed with restricted maximum likelihood models (REML). Year and territory identity, which pooled data from individuals of the same group, were fitted as random factors. Potential explanatory variables that gave nonsignificant results ($P > 0.1$) were sequentially removed until the model included only those terms for which elimination would have significantly reduced the explanatory power. Significant probability values were derived from having all significant terms fitted in the model together, whereas those of nonsignificant terms were obtained from having all significant terms in the model and each nonsignificant term fitted individually (Crawley 2002; Russell et al. 2003). In the Results, values for nonsignificant interactions are omitted.

To test the effect of year-round food supplementation on individual provisioning rates (calculated as the average number of feeding events/h in all observation sessions), we fitted the following explanatory variables: experimental

treatment (fed/unfed), breeding status (breeder/helper), sex, brood size during the 5-day observation period (no brood reductions occurred), number of caregivers, breeding status \times experimental treatment, sex \times experimental treatment and breeding status \times number of caregivers. To test the effect of year-round food supplementation on body mass at the beginning of the nesting period we fitted the following explanatory variables: experimental treatment (fed/unfed), breeding status (breeder/helper), sex, breeding status \times experimental treatment and sex \times experimental treatment.

RESULTS

Although brood size did not differ between experimental and control territories (fed territories: $\bar{X} \pm SE = 3 \pm 0.48$; unfed territories: 2.9 ± 0.28 ; Student's t test: $t_{19} = -0.13$, $P = 0.9$), helpers from territories that were food supplemented year round increased their provisioning effort compared to unfed ones. Conversely, breeders did not respond to the experimental augmentation of resources (Table 1, Fig. 1). This difference was significant, as shown by the interaction between breeding status and experimental treatment in the REML. Individual provisioning rates of both breeders and helpers increased with brood size. There was a marginally nonsignificant interaction between breeding status and number of caregivers. Furthermore, the present data set also showed qualitatively that breeders work harder than helpers, regardless of the experimental treatment (feeding rate: $\bar{X} \pm SE = 3.51 \pm 0.26$ and 1.4 ± 0.2 , respectively; Fig. 1). From the statistical point of view, the REML is not suitable for estimating the significance level of the main effect of the breeding status, because of its interaction with the experimental treatment (Engqvist 2005). Further analyses, however, would be redundant because this pattern has been already well documented in this population (e.g. Canestrari et al. 2005).

Initial Body Mass

At the beginning of each breeding season, body mass of group members did not depend on the food supplementation treatment (unfed weight: $\bar{X} \pm SE = 494.6 \pm 7.94$ g, $N = 35$; fed weight: 508.9 ± 10.56 g, $N = 16$; Wald/ $df = 1.5$, $df = 1$, $P = 0.22$). Breeders were heavier than helpers (breeders: $\bar{X} \pm SE = 530.3 \pm 7.89$ g, $N = 26$; helpers: 467.58 ± 9.84 g, $N = 25$; Wald/ $df = 35.17$, $df = 1$, $P < 0.001$), and males were heavier than females (males: $\bar{X} \pm SE = 524.47 \pm 6.91$ g, $N = 37$; females: 477.92 ± 13.41 g, $N = 14$; Wald/ $df = 34.27$, $df = 1$, $P < 0.001$). Interactions were not significant.

DISCUSSION

Year-round Habitat Quality and Cooperation at the Nest

Our study suggests a role of year-round territory quality in shaping cooperation at nest in carrion crows. In a previous experiment on the same population, where territory quality was manipulated only during the breeding season,

Table 1. Factors affecting individual feeding rates: results of a restricted maximum likelihood model

Model terms	Wald statistic	df	P	Random term estimated variance component±SE	Average effect±SE
Territory identity*				0.32±0.57	
Year*				0.06±0.81	
Breeding status	57.04	1	<0.001		
Brood size	17.43	1	<0.001		
Experiment	0.43	1	0.51		
Sex	0.40	1	0.52		
Number of caregivers	0.25	1	0.61		
Experiment*Breeding status	6.25	1	0.01		
Number of caregivers*Breeding status	3.31	1	0.07		
Minimal model					
Constant					3.55±0.49
Breeding status					
Breeders					0
Helpers					-2.46±0.39
Brood size					0.61±0.14
Experiment*Breeding status					
Unfed breeders					0
Unfed helpers					0
Fed breeders					0
Fed helpers					1.5±0.61
Number of caregivers*Breeding status					
Breeders					0
Helpers					0.44±0.24

*Random term.

neither helpers nor breeders increased their provisioning effort (Canestrari et al. 2007; see below). However, helpers responded positively to the availability of food throughout the year (this study), showing the importance of resources during the nonbreeding period in shaping the dynamics of cooperation at the nest. The role of territory quality in promoting delayed dispersal of offspring and family formation has received much attention in the last few decades. The prediction of theoretical models (Emlen 1995; Kokko & Lundberg 2001) that, within a population, territory resource wealth may favour offspring philopatry has been fulfilled in compelling experimental studies (Komdeur 1992; Dickinson & McGowan 2005). In birds, juvenile delayed dispersal allows kin-based cooperation

at the nest to arise, because commonly only offspring that stay at home can help their parents. Therefore, territory quality ultimately influences the amount of help that breeders can receive.

This proved to be true in crows, where territory conditions during the nonbreeding season influence juvenile natal dispersal (Baglione et al. 2006). However, our results indicate that year-round territory quality may influence cooperation at the nest in a more direct way, that is, by increasing helpers' willingness to provide care to the young. The importance of holding a good territory year round for crows is therefore threefold, as it enhances (1) reproductive success (Canestrari et al. 2008), (2) recruitment of helpers, through increased offspring philopatry (Baglione et al. 2006) and (3) helpers' provisioning effort. This might explain why, in crows, in spite of a rather high competition for breeding territories (Baglione, et al. 2005), some vacancies remained unfilled every year (V. Baglione, unpublished data). Queuing for preferred territories is not an uncommon strategy among group-living birds (Kokko & Ekman 2002) and it has been shown to increase survival and lifetime reproductive success in some species (Ekman et al. 2001). We suggest that a further benefit of acquiring a high-quality territory in cooperatively breeding species is that of securing more aid from auxiliaries at the nest. Such benefit can be substantial in species such as carrion crows, where helpers enhance the reproductive success of the group (Canestrari et al. 2008) and allow breeders to reduce their workload (Canestrari et al. 2007).

Our study also indicates that to understand cooperative breeding in birds fully we may need to widen our focus on conditions during the nonbreeding season. Although

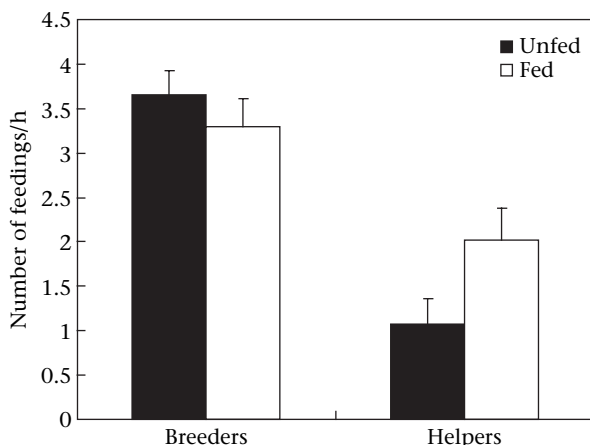


Figure 1. Mean ± SE number of feedings/h by fed and unfed crows.

most social bird species live in stable groups that occupy all-purpose territories year round, most studies so far have typically focused only on the reproductive season, with few exceptions (Cullen et al. 1996). As a consequence, the effect that environmental conditions and social interactions throughout the year may have on cooperation at the nest has so far has been overlooked. We believe that future studies should fill this gap to improve our general understanding of cooperation at the nest.

Provisioning Decisions under Variable Resources

In crows, individual provisioning effort is strongly influenced by current direct fitness benefits: genetic parents show the highest contribution to nestling feeding compared to nonbreeding helpers, who can only pursue indirect fitness benefits or future benefits (e.g. group augmentation) from allofeeding (Canestrari et al. 2005). However, current benefits alone cannot explain the results of this study, where helpers, but not breeders, responded to an experimental long-term increase of territory food resources by augmenting their investment in the current brood.

Chick care is energetically demanding for crows, which lose weight proportionally to their investment in provisioning, regardless of their breeding status (breeders versus helpers), sex or age (Canestrari et al. 2007). Such immediate costs constrain provisioning effort of both breeders and helpers, who reduce mass loss rather than increasing feeding rates when conditions are temporarily favourable (experimental food supplementation during the nesting period). These findings are consistent with the view of chick provisioning as a life history trait where individual strategies respond to a trade-off between current and future reproduction (Heinsohn & Legge 1999). The present study uncovers the complexity of this trade-off, showing a threshold of resource availability beyond which helpers, but not breeders, increase the feeding rate of the current brood. Year-round food abundance could influence helpers' decisions through improved conditions at the beginning of the breeding season that allow helpers to invest more without losing a lot of weight. This, however, seems unlikely, because body mass at the start of reproduction did not vary between fed and unfed crows, but further information on helpers' weight loss throughout the nestling period is needed to explore this mechanism further. An alternative is that helpers that live in year-round high-quality territories are willing to provision more because the prospects for compensating for their energetic losses after the breeding season are good.

Irrespective of the mechanisms, the lack of response of breeders to improved conditions year round is intriguing. Some biparental bird species increase the investment in the current brood when food is abundant (Weimerskirch et al. 2001). In crows, moreover, breeders gain the highest fitness benefits from the current brood, and should therefore be more likely than helpers to increase provisioning after the experimental food supplementation. We suggest that the different prospects for future reproduction for

helpers and breeders are important for understanding this pattern. Every year, breeders have on average a 0.75 probability of retaining their dominant reproductive position until the following breeding season. Conversely, the average probability of nonbreeders being recruited into the reproductive population is only 0.43 (Baglione et al. 2005), being smallest for crows younger than 3 years, which have rarely been observed reproducing in our study population (10 2-year-old breeders observed out of 107). Therefore, the prospects for breeding in the following year are on average better for breeders than for helpers. Both breeders and helpers are expected to invest in self-maintenance until a survival threshold is reached. Beyond this threshold, breeders will need to accumulate further resources to face the probably high provisioning effort of the next breeding attempt, while helpers may be able to afford to increase their current chick provisioning. Our data fit into this scenario. Furthermore, the importance of self-maintenance for breeders is also supported by the tendency of breeders, but not of helpers, to decrease their contribution when the number of caregivers increased, in accordance with previous results that suggest a load-lightening effect of the presence of multiple carers (Canestrari et al. 2007).

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