Behavior of kestrels feeding on frugivorous lizards: implications for secondary seed dispersal

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Secondary seed dispersal is a multistep system that includes 2 or more dispersal processes that can increase the distance from which seeds arrive. This phenomenon is relatively common in some habitats of subtropical oceanic islands due to the frequent frugivore–predator interactions found in them. In this study, we describe how the Eurasian Kestrel is an effective disperser of plants in the secondary seed dispersal process, through interaction with frugivorous lizards. Experiments using captive wild kestrels, along with field data, showed that predation of kestrels on lizards leads to a secondary seed dispersal with 2 possible outcomes: 1) most seeds (89%) are not consumed by kestrels because they reject the lizards' digestive tracts and so receive only the gut treatment of lizards and 2) a small fraction of seeds (11%) appeared inside the kestrel pellets as a result of indirect ingestion by this raptor, thus undergoing double gut treatment. So, 2 different seed dispersal distances may result from this interaction: 1) when the kestrels capture the lizard and transport it to a perch where the seed-containing guts are discarded and 2) when they indirectly ingest a few seeds from lizards, consequently increasing the dispersal distance. Seeds from the Macaronesian plant species *Rubia fruticosa* were tested, finding that those passed through kestrels had a lower germinability than those that remained inside the rejected lizards' digestive tracts, which had similar germination rates to those from control plants (uningested seeds). The kestrel can be considered an important and effective long-distance seed disperser due to the high abundance of frugivorous lizards in their diet, their stereotyped consumption behavior, and the effectiveness of their seed dispersal. *Key words:* Canary Islands, diplochory, endozoochory, frugivorous lizards, long-distance seed dispersal, predatory behavior, seed germination. *[Behav Ecol 20:872–877 (2009)]*

Secondary seed dispersal or diplochory occurs whenever a seed is dispersed in 2 or more different dispersal events by different dispersal agents (Vander Wall and Longland 2004). Both abiotic (e.g., wind and water) and biotic agents (e.g., scatter hoardings, birds, or mammals) could combine, giving rise to different kinds of secondary seed dispersal processes (Forget and Milleron 1991; Levey and Byrne 1993; Vander Wall 2002; Pizo et al. 2005). Diplochory can be adaptive, as a consequence of the increased dispersal benefits that reduce seed mortality (Vander Wall and Longland 2004). These seed dispersal processes often permit the plants to move long distances and are crucial to determining genetic structure, range expansion rates, or the colonization of new habitats (Cain et al. 2000; Nathan 2006). Most of these systems only involve a single seed digestion process, whereas the other step occurs outside the animal (exozoochory) (Ridley 1930). However, secondary seed dispersal can be more complex, especially if a second seed digestion process is mediated through frugivore–predator interaction (double endozoochory). Vertebrate frugivores are often preyed on by predatory birds, which may act as secondary seed dispersers (Ridley 1930; Van der Pijl 1982). Although a few specific descriptive contributions have been published on this matter (Damstra 1986; Hall 1987; Dean and Milton 1988; Nogales et al. 1996), many ecological aspects of this multistep process remain largely unknown.

Double endozoochory occurs in secondary seed dispersal processes of continental systems, where frugivorous birds act as primary seed dispersers and are predated on by raptors (Ridley 1930). However, in subtropical oceanic islands where frugivorous lizards are extraordinarily abundant (Olesen and Valido 2003), these reptiles are also frequently preyed on by raptors and unspecialized predatory birds (Padilla et al. 2007). This is the case of the Canary Islands, where 7 extant frugivorous lizard species of the endemic genus *Gallotia* are distributed over the islands and main islets (Nogales et al. 2001). These lizards are often preyed on by the Eurasian Kestrel (*Falco tinnunculus*) and Southern Grey Shrike (*Lanius meridionalis*) (Carrillo et al. 1994; Padilla et al. 2005, 2007). Lizards thus act as primary seed dispersers, whereas predatory birds are secondary dispersers.

Three studies have been carried out to analyze these complex seed dispersal systems involving at least 3 different plant species (*Lycium intricatum*, Solanaceae; *Rubia fruticosa*, Rubiaceae; and *Asparagus nesiotes*, Convallariaceae), which have been recorded as being dispersed secondarily by shrikes and kestrels (Nogales et al. 1998, 2002, 2007). However, in *Lycium* and *Rubia*, seed treatment in kestrel guts caused a significant reduction in seed germination with respect to control seeds, seeds ingested by lizards, and those secondarily dispersed by shrikes (Nogales et al. 2007). The simultaneous analysis of several ecological variables (number of undamaged seeds, viability, germination, or microhabitat deposition) supports the hypothesis that diplochory by double endozoochory could play a more important role in long-distance seed dispersal than currently recognized, in the colonization of both recent lava flows (Nogales et al. 2007) and other islands (see Moore 1999).

The effect of kestrels in secondary dispersal of indirectly ingested seeds has so far been studied by focusing on some ecological and evolutionary aspects; however, the role of other factors remains largely unknown. This is the case of feeding behavior in predatory birds. It is known that shrikes very often swallow their prey entirely because their small body size means that they can capture only small and medium-sized lizards (mean snout–vent length [SVL]: 74 ± 19 mm), whereas kestrels prey on larger lizards (mean SVL: 94 ± 21 mm) (Costantini et al. 2007; Padilla et al. 2007). The Eurasian Kestrel usually dismembers its lizard prey discarding the digestive tracts (containing seeds), which are often found on their perches (Padilla DP, personal observation). Thus, as a consequence of prey handling, the true overall significance of this raptor in the secondary seed dispersal processes is unknown. Similarly, the fraction of seeds remaining inside the lizards' digestive tracts (single digestive process) compared with that indirectly ingested by kestrels (2 processes) is unclear. So, animal behavior and seed characteristics (e.g., seed coat thickness and hardness) are important factors that can be used together, to predict seed dispersal processes.

The main objective of this work was to determine the ecological role of predation by Eurasian Kestrels in seed dispersal in island ecosystems, for which we studied 1) their behavior when feeding on frugivorous lizards in the field and its effects on secondary seed dispersal processes; 2) the influence on germination of seed passage through reptile and kestrel guts; and 3) predation behavior in captivity on different sizes of lizards, quantifying the number of seeds subjected to 1 or 2 digestive processes.

METHODS

Study area

The Canary Islands (27°37′–29°25′N and 13°20′–18°19′W) are of volcanic origin and located 100 km off the Atlantic coast of northwest Africa. Fieldwork was carried out on Tenerife, the largest (2034 km^2) and highest (3718 m above sea level [a.s.l.]) island in the archipelago, with clearly defined vegetation formations according to altitude. The lowlands of this island are characterized by a xeric climate with an annual mean temperature of about 21 °C and a mean annual rainfall between 100 and 400 mm, mainly between October and February (Marzol Jaén 1988). Vegetation consists of a sparse xerophytic shrub cover, dominated by *R. fruticosa* (Rubiaceae), *Euphorbia obtusifolia* and *Euphorbia canariensis* (Euphorbiaceae), *L. intricatum* and *Withania aristata* (Solanaceae), *Periploca laevigata* (Asclepiadaceae), and the alien *Opuntia* spp. (Cactaceae).

Rubia fruticosa is a shrub endemic to the central Macaronesian archipelagos (Madeira, Salvagens, and the Canaries). It is distributed in the lowlands of all the Canary Islands and can reach a mean plant cover of about 0.5 m^2 and 0.5 m in height. It produces spherical fleshy fruits, translucent berries with an average length of 7.5 mm, a diameter of 5.6 mm, and a water content of 81.5% ($n = 40$ fruits). Each berry contains an average of 1.4 spherical seeds and the average seed weight is 8.2 mg (Nogales et al. 1999). Fruits of *R. fruticosa* are eaten by a variety of vertebrates, which include native lizards and birds (legitimate dispersers) and introduced alien mammals (illegitimate dispersers) (Nogales et al. 2005). Moreover, seeds of this species can be indirectly dispersed by kestrels and shrikes, when these prey on the frugivorous lizards (Nogales et al. 2007).

Fieldwork and experimental procedures

Fieldwork was carried out in north Tenerife (spring 2006) in 9 different localities where *R. fruticosa* was present, coinciding with 15 Eurasian Kestrel breeding territories. Control seeds were obtained from a total of 200 fruits collected directly from the mother plants ($n = 40$), to evaluate the effect on germination in comparison with those seeds that passed through the different gut treatments. Five fruits per plant were taken in order to provide a suitable representation of the different plant populations. A total of 600 lizard droppings, 660 kestrel pellets, and 36 lizard guts rejected by kestrels were collected, a similar number from each of the 15 kestrel territories. All these samples were fresh and were used to quantify the seeds indirectly dispersed by kestrels in the wild and to evaluate the effect on germination of gut passage through the different dispersers. Each dropping, pellet, and lizard gut was treated separately and seeds were manually extracted and counted.

A germination experiment was conducted in a greenhouse where the same conditions were applied to all treatments for 6 months (1 October 2006 to 31 March 2007). A total of 190 seeds from mother plants (controls), 230 from lizard droppings, 101 from kestrel pellets, and 119 from lizards' digestive tracts were randomly and independently sown 5 mm deep with each seed in a separate 4-cm^2 pot containing a standard substrate (50% peat and 50% agricultural soil). All pots were watered every 2 days, and germination was monitored every 5 days by recording newly emerged seedlings. The experiment was performed at Tagoro (north Tenerife; 300 m a.s.l.), a site with similar climatic conditions as those found in the study areas.

Captivity procedures

To evaluate the predatory behavior of the Eurasian Kestrel on frugivorous lizards, experiments were carried out in captivity (spring–summer 2007). Five wild kestrels (1 adult and 1 juvenile of each sex and 1 subadult male) were temporarily maintained in captivity at the Wildlife Rehabilitation Centre (La Tahonilla, Cabildo de Tenerife) after recovering from different types of injuries. During the experiment, all birds were in perfect physical condition and ready to be released. Captivity tests took place in a pen (3.5 × 3 × 3 m) with a perch at a height of 1.90 m across the shortest side of the pen. Each kestrel was tested individually, and all predation sequences were recorded with a video camera connected to an external TV.

Kestrels were fed once daily with a lizard (*Gallotia galloti*) that was placed in the pen. These experiments were performed in accordance with the recommendations of Huntingford (1984) and the Association for the Study of Animal Behaviour Society (2001). The number of lizards offered to kestrel during the experiments was kept to a minimum to generate adequate sample sizes. All experiments and lizard captures were carried out under the supervision and approval of the Spanish authorities (Cabildo de Tenerife, register no. 62.626). A total of 30 lizards were used in the experiment (6 per kestrel). Lizards were captured using pitfall traps, and each one was kept independently in terrariums (1 × 1 m) for not more than 2 days before offering them to the kestrels. Different lizard sizes were employed according to kestrel prey size selection in Tenerife (Padilla et al. 2007). To determine if kestrels changed their prey handling in relation to lizard sizes and if this could influence the number of seeds indirectly ingested by the kestrels, lizards were classified into 3 size categories (SVL—small, 60 to 81 mm; medium, >81 to 101 mm; and large, >101 to 131 mm). Each size category was offered in a similar proportion to each kestrel.

Before lizards were offered to the kestrels, each one was measured, weighed, and force-fed by hand with a specific color of glass beads that were similar in size to *R. fruticosa* seeds. Different colored beads were used instead of seeds, so that we

could precisely identify the beads coming from each lizard. A total of 15 beads were fed to small lizards, whereas 20 beads were fed to medium- and large-sized lizards due to the gut volume of each size (Nogales M, unpublished data). The time interval between bead ingestion by lizards and their later predation by kestrels was recorded to assess its potential influence on the number of seeds that appeared inside kestrel pellets (double endozoochory) or inside the rejected lizards' digestive tracts (single endozoochory). Before different lizard sizes were offered to the kestrels, the time that glass beads remained inside the lizards, periods of 24, 12, 6, 3, and <1 h, was accurately monitored.

The following days after each lizard was consumed by a kestrel, both lizard remains (heads and guts) and kestrel pellets were collected and analyzed to determine the fate of glass beads previously introduced into the lizards.

Data analysis

Contingency analyses were used to evaluate the number of seeds found in lizard droppings, kestrel pellets, and lizards' digestive tracts from predation. We employed these analyses to gain an overall view of the data, owing to the different sizes, origin, and nature of the seed-containing samples analyzed (lizard droppings, kestrel pellets, and lizards' digestive tracts). Seed germination from the different treatments (control, lizards, kestrel pellets, and lizards' digestive tracts) was analyzed by likelihood ratio tests. When the same data set was used, a posteriori correction of significance by a sequential Bonferroni procedure was applied. To evaluate the number of beads that appeared in kestrel pellets and inside lizards' digestive tracts after predation events in captivity, a non-parametric test (Wilcoxon matched pair) was performed using the average of each kestrel in order to avoid pseudoreplication bias. This test was used because the data did not meet the requirements of a parametric test, even after transformations, and also because the number of beads appearing in pellets was clearly related to that found in the lizard guts. Influence of lizard size and the time period of beads inside lizards before predation, in relation to those beads found in the rejected lizard guts or kestrel pellets, were tested using a 2-level nested design analysis of variance, where the different kestrels were considered as a fixed factor. All data were analyzed with the SPSS (v. 15.0) software.

RESULTS

Seed movements and germination

Analysis of kestrel pellets in north Tenerife demonstrated the importance of lizards in the diet of this raptor with 63% of its pellets containing 1 or more lizards. All the *R. fruticosa* seeds that appeared inside kestrel pellets were associated with lizard remains. As a consequence of kestrel prey-handling behavior, numerous lizards' digestive tracts with a high number of *R. fruticosa* seeds inside them, usually associated with lizard heads, were found on their perches. The greatest number of seeds per sample was found in lizards' digestive tracts, followed by lizard droppings, whereas the lowest number was recorded in kestrel pellets ($G = 389.29$, degrees of freedom (df) = 2, $P < 0.001$) (Table 1).

A significantly greater number of control seeds germinated than seeds extracted from lizard droppings ($G = 8.80$, df = 1, $P = 0.003$). However, no differences were observed between control seeds and those coming from lizards' digestive tracts ($G = 0.82$, df = 1, $P = 0.36$). No differences in germination percentage were observed between seeds from lizards' digestive tracts and those from lizard droppings ($G = 2.68$, df = 1, $P = 0.101$). Finally, seeds from kestrel pellets had a clearly

Table 1

Seeds from *Rubia fruticosa* found in lizard droppings, kestrel pellets, and lizards' digestive tracts rejected by kestrels, as a consequence of their feeding behavior in Tenerife, Canary Islands

Sample type (treatment)	Seeds[a] (mean ± standard deviation)	%[b]	Total[c]	n[d]
Lizard droppings	0.97 ± 3.52	14.7	583	600
Kestrel pellets	0.15 ± 0.68	7.12	101	660
Lizards' digestive tracts	3.30 ± 8.33	25	119	36

[a] Number of seeds per sample.
[b] Frequency of occurrence.
[c] Total number of seeds found.
[d] Number of samples analyzed.

lower germination percentage in comparison with all treatments ($P < 0.001$, for all comparisons) (Figure 1).

The germination ratio of seeds from kestrel pellets to that of seeds from rejected lizards' digestive tracts was 1:27 (Figure 1).

Captivity tests

All kestrels showed the same behavior when feeding on lizards. In all cases ($n = 30$ trials), kestrels decapitated the lizards and then rejected the lizards' digestive tracts (from stomach to cloaca).

After the predation experiment, the total number of glass beads (simulating seeds) introduced into the lizards were recovered. Of this total number, after the prey handling by kestrels, a significantly higher number of beads appeared inside the rejected guts (89%) with respect to that in kestrel pellets (11%) ($Z = -2.02$, $P = 0.043$). The number in guts and pellets was not significantly influenced by lizard size ($F_2 = 3.91$, $P = 0.058$ and $F_2 = 0.67$, $P = 0.52$, respectively), despite a slight increase in the number in pellets after preying on small lizards (Figure 2a). Moreover, those beads found in guts and pellets were not influenced by the particular behavior of each kestrel ($F_8 = 0.64$, $P = 0.72$ and $F_8 = 0.27$, $P = 0.96$, respectively).

Finally, the length of time between seed ingestion by lizards and their subsequent predation by kestrels had a great influence on the number of beads found in lizards' digestive
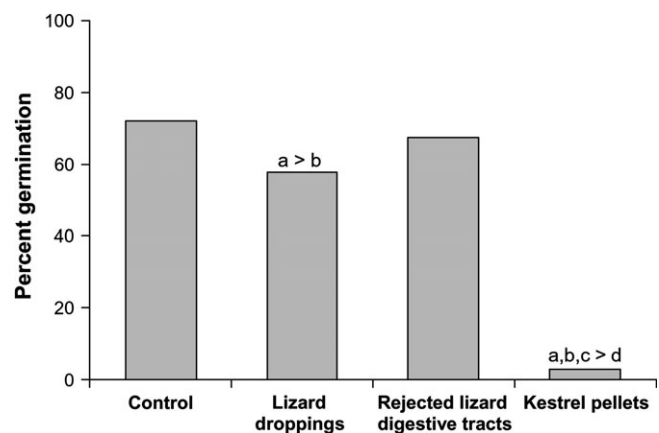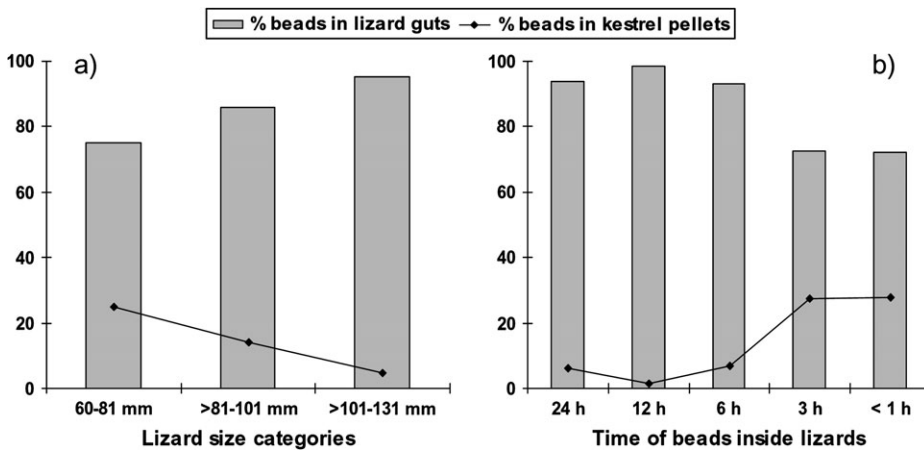

Figure 1
Seed germination of *Rubia fruticosa* of the different treatments. Significant differences in seed germination are indicated with the letters: a, control seeds; b, seeds from lizard droppings; c, seeds from rejected lizards' digestive tracts; and d, kestrel pellets.

Figure 2
Influence of kestrel feeding behavior on the secondary seed dispersal processes tested in captivity, taking into account the proportion of beads that appeared in kestrel pellets (lines) and inside lizards' digestive tracts (bars): (a) after predation on different sized lizards and (b) monitoring the time elapsed between bead ingestion by lizards and their subsequent predation by kestrels.

tracts and kestrel pellets (Figure 2b). When we compared the number of beads that appeared in pellets after the different time periods, 4 times more beads were found in pellets when they had been inside the lizards for 3 h or less ($F_4 = 5.13$, $P = 0.031$).

DISCUSSION

Secondary seed dispersal

Our findings provide evidence for a newly discovered process of secondary seed dispersal by kestrels that include a single event of endozoochory. After the capture of frugivorous lizards by kestrels and the subsequent movement to their perch, this raptor acts as an effective secondary seed disperser due to its particular prey-handling technique when they reject the lizards' digestive tracts.

Seed dispersal effectiveness is of crucial importance in the survival and regeneration of plants. It is influenced by factors such as the passage of seeds through the frugivores' digestive tracts, the number of seeds transported by the dispersal agent, or the seed shadow (Schupp 1993). On islands, reptiles play an important role as seed dispersers of a wide variety of plants (Olesen and Valido 2003), and the Canary Islands harbor clear examples of this process. This archipelago supports a high abundance of frugivorous lizards (genus *Gallotia*), mostly due to their lower predation risk and competition pressures as well as their broader trophic niche (Olesen and Valido 2003). Indeed, these reptiles constitute important key resources for predators such as kestrels and shrikes (Padilla et al. 2007). Previous studies have demonstrated that these 2 birds act as secondary seed dispersers after preying on frugivorous lizards (Nogales et al. 1998, 2002, 2007). Such studies report the phenomenon of double endozoochory found in 3 plant species (*Lycium*, *Rubia*, and *Asparagus*) with different seed hardness and sizes. The different physiological treatments on seeds caused by passage through kestrels and shrikes produce diverse effects on viability and germination. Only the hard seeds of *Asparagus* survived the raptor gut passage, whereas shrikes did not negatively affect seed viability and germination of any of the 3 plant species (Nogales et al. 2007).

Our results show that *R. fruticosa* seeds were found to some extent in the kestrel pellets, although most were found in the numerous lizards' digestive tracts that kestrels left behind at the time of feeding. Thus, kestrel predation leads to secondary seed dispersal with 2 potential seed fates: 1) most of seeds are not consumed by kestrels as they are rejected along with the lizards' digestive tracts, undergoing a single (lizard) gut treatment, whereas 2) a few seeds are indirectly ingested by

kestrels, undergoing a double gut treatment. Nogales et al. (2007) found that the lizard–shrike interaction transported the highest proportion (68%) of the total number of seed samples, followed by seeds directly dispersed by lizards (29%), and the lowest number of seeds was found after the lizard–kestrel interaction (3%). This study underestimated the number of seeds found in this latter interaction because only the number of seeds appearing in kestrel pellets was recorded, without taking into account the seeds remaining in the discarded lizards' digestive tracts.

Seed germination

This process can be greatly influenced by the morphological and physiological characteristics of the frugivore digestive systems and other closely related factors such as seed retention time or percentage of seed coat scarification (Jordano 1992; Traveset 1998; Rodríguez-Pérez et al. 2005). In this study, *R. fruticosa* seeds found inside kestrel pellets clearly had a lower germination percentage. These data are in agreement with those obtained by Nogales et al. (2007), so most *R. fruticosa* seeds are unable to resist the strong enzymatic action and long gut passage time (GPT) of this diurnal raptor. However, we show that most seeds remain inside the rejected lizards' digestive tracts due to the prey-handling behavior. These rejected tracts remain in the field for only a few days because ants eat practically all of them and, consequently, the seeds are released into the field (Padilla DP, personal observation). Such seeds retained a similar germination capacity to those from control plants and even greater than those dispersed directly by lizards. The higher germination percentage of seeds found in lizards' digestive tracts compared with those in lizard droppings might be because their gut transit time has been shortened by the death of the lizards. Furthermore, seeds dispersed by lizards (*G. galloti*) had a significantly reduced germination rate with respect to control seeds. This could be due to their relatively great SVL (mean: 106.4 ± 12.1 mm) and GPT (mean: 6.9 ± 3.8 days; Valido and Nogales 2003), which could reduce the seed viability of *R. fruticosa*. However, in Nogales et al. (2007), no differences in germination were observed between seeds from lizard droppings (*Gallotia atlantica*) and control seeds. *Gallotia atlantica* is a smaller lizard (SVL, mean: 60.8 ± 9.9 mm) with shorter GPT (GPT, mean: 2.4 ± 1.5 days; Valido and Nogales 2003) and with less impact on seed viability.

Taking into account the germination data and the high proportion of seeds found inside lizards' digestive tracts, it is plausible to conclude that the kestrel is in fact an effective secondary seed disperser in the Canary Islands, in a similar

way to the Southern Grey Shrike, which was considered the most efficient secondary seed disperser in the Canary Islands (Nogales et al. 1998, 2002, 2007). For this reason, we suggest that this raptor may be a legitimate secondary seed disperser of the many different plant species dispersed directly by lizards in the Canaries. These lizards, of genus *Gallotia*, are considered to be one of the most important seed dispersers, often with more than 50% of their diet volume consisting of fleshy fruits (Valido and Nogales 1994; Olesen and Valido 2003; Rodríguez et al. 2008).

Predatory behavior in captivity

Our observations in captivity have demonstrated the importance of the way in which kestrels prey on frugivorous lizards and its influence on secondary seed dispersal. In all cases, the same conduct was observed, showing that lizard size did not influence the predatory behavior. This prey handling appears to be a stereotype, in which kestrels decapitate the lizards and then reject the lizards' digestive tracts. Other captivity studies also demonstrated that prey size does not modify the predation technique (Csermely et al. 1989; Csermely 1994). Our experiments indicate that the vast majority of seeds that occur inside the live lizards are later found in the rejected digestive tracts after the lizards are eaten. In contrast, only a few seeds would be subjected to a double digestion, subsequently appearing in kestrel pellets. The number of seeds dispersed secondarily by kestrels in interaction with frugivorous lizards is therefore clearly higher than those estimated by Nogales et al. (2002, 2007). Nevertheless, the number of seeds found in kestrel pellets depends on the time elapsed between seed ingestion by lizards and their later predation by kestrels. A higher number of seeds pass through a double digestion process, subsequently appearing in kestrel pellets, when the lizards eat the fruits 3 or less hours before the predation. During the predation, kestrels eat 2 muscular parts (pharynx and esophagus) of the lizards' digestive tracts. Seeds that are later found in kestrel pellets are probably those, which are still inside these tissues. Herbivorous lizards like *G. galloti* have a long transit time to increase digestive efficiency because they do not show specific anatomical traits for digestion of cellulose (Throckmorton 1973; Christian et al. 1984; Zimmerman and Tracy 1989; Valido and Nogales 2003).

Implications for long-distance seed dispersal systems

Long-distance dispersal (LDD) of plants includes rare and highly stochastic ecological events that are often difficult to detect and quantify (Higgins and Richardson 1999; Clark et al. 2001; Nathan 2006). The morphology and physiology of the dispersal units are adapted for movement by standard dispersal vectors; this is defined as a syndrome of dispersal (Van der Pijl 1982). However, a high number of plant species could move long distances due to the action of nonstandard agents (Higgins et al. 2003). In the case of fleshy fruits in subtropical oceanic islands, for instance those from *R. fruticosa*, seeds are mainly dispersed by passerines and lizards (standard dispersers) (Nogales et al. 2005). Nevertheless, nonstandard dispersers, such as kestrels and shrikes, can play an important role in LDD events when they prey on the frugivorous lizards (Nogales et al. 2007). For this reason, kestrels, with average movements of approximately 500 m (Nogales et al. 2007), can be considered an important and effective LDD vector due to the high abundance of lizards in their diet and the effectiveness of their seed dispersal, respectively. Two different seed dispersal distances may result 1) when kestrels capture the lizard and transport it to a perch where the seed-containing guts are discarded and 2) when they indirectly ingest a few

seeds from lizards, subsequently increasing the dispersal distance. The second type can only be considered effective when seeds resist scarification despite the long retention time (12–23.5 h) and the strong enzymatic gut effect of this diurnal raptor. Finally, the data presented in this study demonstrate how useful animal behavior studies can be in explaining differential dispersal and potential seed distribution and how nonspecialized animals can be effective dispersers, often being responsible for LDD of plants.

CONCLUSIONS

Little attention has been given to the importance of raptors as seed dispersers in reviews of plant–animal interactions (Snow B and Snow D 1988; Fleming and Estrada 1993; Levey et al. 2001; Herrera and Pellmyr 2002; Dennis et al. 2007). However, raptors could play a valuable role as primary dispersers when they eat fruits directly (Galetii and Guimarães 2004) or as secondary seed dispersers when they prey on frugivorous animals (Galetii and Guimarães 2004; Nogales et al. 2007). The study of feeding behavior of the dispersers is also a key to understanding the true effectiveness of the seed dispersal processes. The present study changes the concept of the Eurasian Kestrel as an ineffective secondary seed disperser as previous studies tended to conclude. Now, this raptor can be considered a common and effective secondary seed disperser due to its particular prey-handling technique. They prey on frugivorous lizards, carry them to their perch, and finally reject the lizards' stomach and intestines, in which the seeds undergo only 1 digestion process. Due to this, most seeds retain high viability after the secondary dispersal process, allowing the plants to be spread long distances away from the mother plants.

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