

## LETTER

# Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment

Orr Spiegel\* and Ran Nathan  
 Movement Ecology Laboratory,  
 Department of Evolution,  
 Systematics and Ecology,  
 Alexander Silberman Institute of  
 Life Sciences, The Hebrew  
 University of Jerusalem, Givat  
 Ram, Jerusalem 91904, Israel  
 \*Correspondence: E-mail:  
 ors@pob.huji.ac.il

## Abstract

Fleshy-fruited plants are usually dispersed by an array of frugivores, differing in the effectiveness of the dispersal service they provide to the plant. Body size differences among frugivores are hypothesized to affect seed dispersal distances and consequently their effectiveness as dispersers. We tested this hypothesis by comparing the effectiveness of two passerine birds, grackles (*Onychognathus tristramii*) and bulbuls (*Pycnonotus xanthopygus*), dispersing the desert shrub *Oc Bradenus baccatus*. Laboratory experiments, quantifying gut retention time and the effect on germination, were combined with field observations quantifying bird movements and fruit consumption rates. An empirically parameterized mechanistic model showed that the two dispersers switch roles as a function of spatial-scale: while most seeds within the local habitat were dispersed by bulbuls, the larger grackles were exclusively responsible for between-patches, long-distance dispersal. We suggest that distance-related differences are common and important to plant fitness, and thus should explicitly be considered in studies of disperser effectiveness.

## Keywords

Arid ecosystems, dispersal curve, fragmentation, frugivory, long-distance dispersal, *Oc Bradenus baccatus*, *Onychognathus tristramii*, *Pycnonotus xanthopygus*, radio telemetry.

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## INTRODUCTION

Seed dispersal and plant-disperser interactions play a major role in determining the spatial structure, dynamics and composition of plant populations and communities (Godínez-Alvarez *et al.* 2002; Levin *et al.* 2003; Levine & Murrell 2003), and have important implications for conservation and management (Trakhtenbrot *et al.* 2005). The post-dispersal seed deposition pattern, interactively with the spatiotemporal heterogeneity in the suitability of establishment sites, acts as a template upon which early recruitment processes operate (Janzen 1970; Schupp & Fuentes 1995; Nathan & Muller-Landau 2000). Patterns of dispersal and establishment are moulded by a range of ecological processes operating at different spatial scales (Kollmann 2000). This general ecological principle (Levin 1992) has been demonstrated in several plant–frugivore systems (e.g. García & Ortiz-Pulido 2004), especially in spatially heterogonous environments in which fleshy-fruited plants are patchily

distributed (Santos *et al.* 1999; Jordano & Schupp 2000; Calviño-Cancela 2002; Revilla *et al.* 2004). Consequently, seed dispersal distance can strongly affect plant recruitment patterns; at the local scale, for example, seeds dispersing beyond the zone of high density-dependent mortality close to the source plant are more likely to survive (Janzen 1970) while at larger scales, rare long-distance dispersal (LDD) events can facilitate colonization of newly opened (Cain *et al.* 2000; Nathan 2006).

Seed deposition patterns are typically generated by various vectors (Loiselle & Blake 1999; Jordano & Schupp 2000; Nathan 2007), which may differ in their dispersal service efficiency (the contribution of a vector to plant fitness; Murray 1988; Schupp 1993; Jordano & Schupp 2000). The concept of *disperser effectiveness* (Schupp 1993) emphasizes the quantitative (number of dispersed seeds) and the qualitative (fate of dispersed seeds and their probability to reach maturity) components of the contribution. This concept has stimulated intensive research, especially on

fleshy-fruited plants dispersed by frugivorous birds and mammals (Graham *et al.* 1995; Sun *et al.* 1997; Loiselle & Blake 1999; Santos *et al.* 1999; Holbrook & Smith 2000; Calviño-Cancela 2002; Clark *et al.* 2005; Martins 2006).

However, thorough comparisons quantifying all components of disperser effectiveness among key frugivores are rare and have either compared frugivores dispersing seeds over similar distances and operating at the same spatial scale (within the same habitat patch), or ignored probable differences in frugivore activity across different scales (between different patches). Yet, frugivores can differ drastically in their capacity to link otherwise-isolated habitat patches in naturally patchy or anthropogenically fragmented ecosystems (Santos *et al.* 1999; Revilla *et al.* 2004; Price 2006; Jordano *et al.* 2007) and therefore may differ in their quality of deposition. Thus, investigating the effect of dispersal distance can critically alter conclusions about disperser effectiveness emerging from 'traditional' studies that not explicitly consider dispersal distances. Santos *et al.* (1999), for example, compared the effectiveness of birds and mammals in dispersing Spanish juniper seeds in a fragmented landscape. Although thrushes were more efficient in some aspects of their dispersal service, foxes were important and efficient dispersers chiefly because of their frequent inter-patch movements have facilitated seed dispersal to fragments of all sizes.

Differences in the distances over which vectors disperse seeds can arise from differences in their taxonomic group, life history traits and foraging behaviour (e.g. Clark *et al.* 2005; Tellería *et al.* 2005). Although this fact is widely acknowledged, it was rarely placed in the context of disperser effectiveness. In this first introduction of dispersal-distance effects into this framework we focus on differences expected from variation in a key life history trait, the frugivore body size. Indeed, dispersal vectors of the same plant species can differ markedly in their size, for example, fruits of *Prunus mahaleb* are dispersed by 19 bird species, ranging from 10 to 500 g in their mean body mass (Jordano & Schupp 2000). Body size is generally positively correlated with home range area (Jetz *et al.* 2004; Makarieva *et al.* 2005), seed retention time in the gut (Karasov 1990; Murphy *et al.* 1993) and fruit consumption per-visit (Jordano 1982; Jordano & Schupp 2000). Thus, all else being equal, larger birds are expected to forage over larger areas and retain seeds in their gut for longer periods and therefore to disperse seeds over longer distances (Westcott & Graham 2000; Jordano *et al.* 2007).

In this study, we quantified all commonly used ('traditional') components of disperser effectiveness, as well as the vector-specific dispersal distance, in a natural frugivore-plant system. We selected a desert ecosystem as a typical naturally patchy landscape, and focused on the dispersal of seeds of a fleshy-fruited perennial shrub (*Ochradenus baccatus*

Delile) by two locally common passerine birds: the yellow-vented bulbul (*Pycnonotus xanthopygos* Hemprich & Ehrenberg, *c.* 40 g) and the Tristram's grackle (*Onychognathus tristramii* Sclater, *c.* 120 g). We hypothesize that different dispersers vary in their effectiveness as function of their body size, and specifically predict that the two species would differ mainly in dispersal distances, expected to be much longer for seeds dispersed by the larger grackles. We tested this prediction by combining field observations, radio telemetry tracking, laboratory experiments of gut retention time and effect on germination, and a simple mechanistic model of seed dispersal by frugivores. We shall demonstrate that while the two species are similar in most 'traditional' components of disperser effectiveness (i.e. quantity of dispersed seeds and the qualitative effect on germination), they differ markedly in seed dispersal distances, thus confirming our prediction. We shall also emphasize the prevalence and importance of spatial scale in the context of disperser effectiveness in patchy environments.

## METHODS

### Study site and species

The study was carried out in the lower part of Wadi Rahaf in the Judean Desert west of the Dead Sea, Israel (31°15' N, 35°22' E). Rainfall occurs only during winter, with annual mean of < 70 mm. The mountainous terrain is crossed by a series of rocky seasonal water courses (wadis) which are few hundred metres (maximal width  $\pm$  SE:  $233 \pm 59$ , range: 50–800 m,  $n = 20$ ) wide, and separated by hostile matrix of few kilometres ( $1.3 \pm 0.2$ , 0.4–3.0 km, 19) apart. Vegetation in the wadi is sparse and dominated by many *O. baccatus* shrubs (Fig. 1). Both avian species are resident and abundant at the study site.

The yellow-vented bulbul (*P. xanthopygos*), a small-sized (35–46 g) passerine, is a common Middle East resident (Cramp 1988; Shirihai 1996). Bulbuls live in pairs or small groups with defined territories and have relatively small home ranges. Bulbuls feed mainly on fruit, supplemented during the breeding season with some arthropods (Cramp 1988).

Tristram's grackle (*O. tristramii*), a medium-sized (98–140 g) passerine, is common in rocky areas along the Dead Sea and Rift Valley (Cramp 1988; Shirihai 1996). Outside the breeding season, grackles live in flocks of 10–50 individuals. They fly long distances (few km) from their breeding or roosting sites to their foraging sites on a daily basis; their varied diet includes fruits, plant parts, insects and anthropogenic garbage (Cramp 1988).

The focal plant species of this study is *O. baccatus* (family: Resedaceae), a perennial shrub, common in the arid parts of Israel and the Middle East. Shrubs bear fruit year-round, with a peak during winter and spring (Wolfe & Shmida



**Figure 1** The study site at the lower part of Wadi Rahaf. The Dead Sea is seen in the background (to the east). Vegetation is confined within the wadi walls and dominated by acacia (*Acacia* spp.) and tamarisk (*Tamarix* spp.) trees. Most of the smaller shrubs visible in the wadi are *Ochradenus baccatus*.

1997). Fruits are rounded, fleshy white berries, 4–6 mm in diameter, containing  $11.3 \pm 0.2$  seeds (mean  $\pm$  SE, range: 7–16 seeds,  $n = 750$  fruit). Although the fruits are consumed by a wide variety of animals, grackles and bulbuls are among the plant's main dispersers in this study area (Altstein 2005; Bronstein *et al.* 2007).

### The quantitative component of disperser effectiveness

Quantities of consumed fruit were determined by observing *Ochradenus* shrubs *in situ* and recording bird feeding events, using digital-video cameras (EDRS400, EverFocus Ltd, Taipei, Taiwan) and a telescope (APO-Televid 77, Leica, Solms, Germany). On 12 observation days between January and May 2005, a group of four fruit-bearing shrubs was randomly selected and observed for approximately 7 h, beginning at 7:00 AM. Altogether, there were 84 h of simultaneous observations on  $3.8 \pm 0.3$  (mean  $\pm$  SE) shrubs, totalling 322 observation hours. For each bird feeding event, the species, visit duration and amount of consumed (swallowed) fruit were recorded. On rare

occasions when two or more birds arrived at a shrub simultaneously, data were recorded separately for each.

### The qualitative component of disperser effectiveness

#### *Quality of treatment – gut passage and germination experiments*

Gut retention time (GRT) and its effect on germination were tested in two sets of standard laboratory experiments (Sun *et al.* 1997; Loiselle & Blake 1999; Holbrook & Smith 2000). Individual birds captured in the Judean Desert were held in standard sized cages (100  $\times$  55  $\times$  45 cm) for up to 1 month. Their physical status and weight were monitored twice a week.

During experiments we used a special apparatus developed to minimize bird stress that may affect the digestive process (Altstein 2005). Four experimental cages (50  $\times$  55  $\times$  45 cm) were placed over a motor-powered conveyor belt, moving faeces to an observer hidden behind a one-sided screen, enabling faeces collection and GRT recording for four birds simultaneously. Birds were allowed 2–3 days of acclimation before each trial and were then transferred to the experimental cages for an overnight where they were supplied only with water. At the beginning of the experiment, the birds were offered 50–70 *Ochradenus* fruit in a remote-controlled Petri dish. The dish was closed 10 min after the first fruit was eaten, allowing the birds to eat most of the fruit. No other food or water was available. Trials began early in the morning and ended half an hour after the last seed was detected or after 7 h (grackles) and 3 h (bulbuls). Using the midpoint of the feeding duration as the starting point (i.e. 5 min after the first fruit was eaten), we calculated GRT as the proportion of defecated seeds in 15-min intervals per bird per trial, averaged for each bird over all trials. Three to five trials were carried out for each of the nine grackles and seven bulbuls, totalling 32 and 21 successful trials, respectively.

Gut passage effect on germination was tested by a second set of experiments. Seeds from the GRT experiment were separated from bird faeces and each seed cohort was transferred to a separate 55 mm Petri dish with absorbent paper. All dishes were irrigated with an initial amount of 2 mL water, and germinated in an incubator (MMM, Munich, Germany) in stable conditions (25 °C, 70% relative humidity, 12 h of daylight), determined previously as favourable for *Ochradenus* germination (Altstein 2005). Germination was checked daily until no germination was found for more than four successive days. Water was added as required and germinated seeds (determined by rootlet emergence) were removed to prevent potential inhibition to other seeds. Two types of controls were used: (i) seeds within intact fruit, six fruit per Petri dish (total of 24 fruit). The actual seed number was counted after fruit were opened by germinating seeds. (ii) Seeds that were manually separated from fruit pulp, 15 seeds

per Petri dish (total of 105 seeds). Fruit collected from various shrubs were mixed and randomly allocated for trials and controls in each GRT experiment.

#### *Quality of deposition*

The small-scale (within wadi) movements of the dispersers were monitored by observations from high vantage points on the wadi wall. To determine the bird position, a system composed of a 3D laser range finder ('LRF'; LaserAtlanta, Norcross, GA, USA), binoculars (10 × 40 Nikon, Tokyo, Japan), a laptop and a GPS unit (12XL, Garmin, Olathe, KS, USA) was used. Measurement accuracy is estimated to have an average error of ± 2 m. In each tracking session, a distinct bird was tracked, and its position and microhabitat (e.g. acacia tree or *Ochradenus* shrub) was recorded every 15 s, starting immediately after the bird was located and ending when it travelled beyond the LRF range (400 m), left the study site, or was lost inside dense vegetation (usually acacia foliage). As birds were unmarked, the tracking session was stopped when the focal bird could no longer be distinguished from other birds. Tracking sessions were not statistically independent, since some sessions are probably repeated measurements on the same birds; yet, the data presumably represent the movements of grackles and bulbuls active in the study site. The observations were performed once a week from December 2004 to May 2005, starting in the early morning to late afternoon. The total observation time was 60 h.

Large-scale (between wadis) movement of the dispersers was monitored by radio telemetry tracking. Birds were captured using mist nets at the study site, weighed and tagged with radio transmitters glued to their backs (grackles: 2.4 g, Sparrow system, Champaign, IL, USA; bulbuls: 0.9 g, Holohil, ON, Canada). Tagged birds were tracked by two to three observers using portable receivers (AR8200, AOR) with Yagi antennas. The bird position was estimated by triangulation using the LOCATEIII software (Nams 2005), every  $35.8 \pm 5.5$  and  $42.9 \pm 12.2$  min (mean ± SE) for grackles and bulbuls, respectively. Nine grackles were tracked for 3–12 days each, during August–September 2004, and 13 bulbuls were tracked for 2–5 days during October–November 2005. Tracking days with < 7 successful locations were excluded from further analysis. Home range estimations were based on Minimum Convex Polygons, using the Hawth's analysis extension tool for ARCVIEW software (Beyer 2004), excluding individuals with < 30 locations.

#### Dispersal curves

A simple mechanistic model was used to generate distance distributions (*sensu* Nathan & Muller-Landau 2000) of *Ochradenus* seeds dispersed by the two avian species. Following standard procedures (Murray 1988; Holbrook & Smith 2000), the model integrates data on GRT, small- and

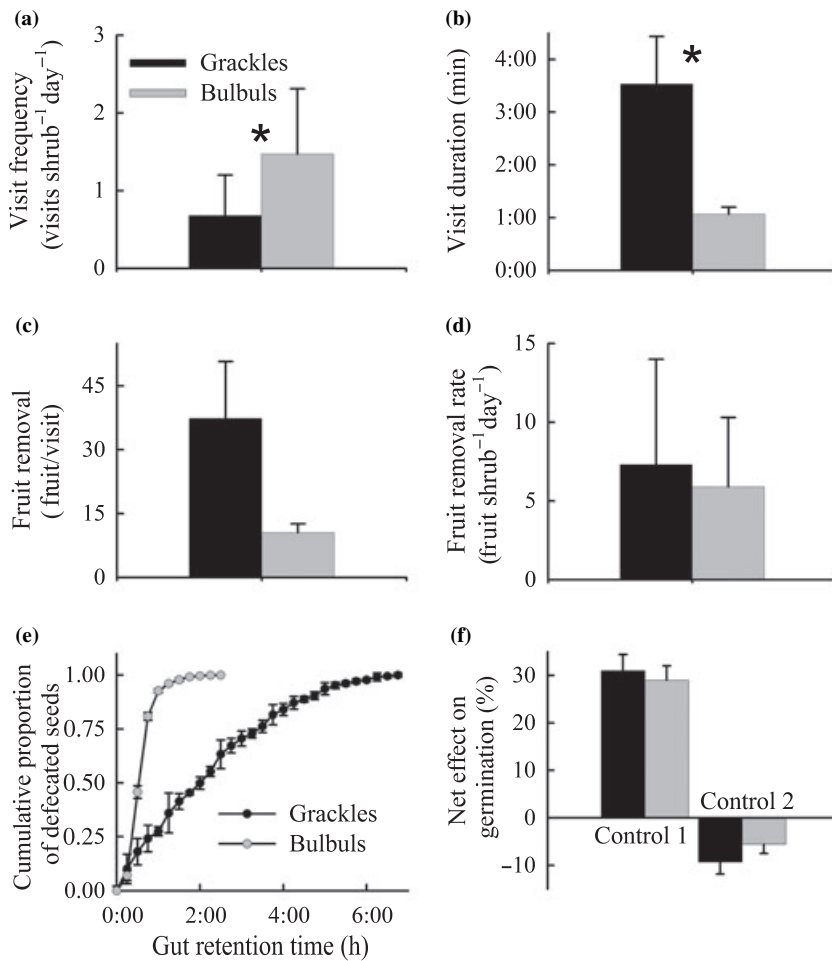
large-scale movements and relative amounts of dispersed seeds.

First, the proportion of defecated seeds for each 15-min interval is randomly selected from the GRT data. This proportion is multiplied by the estimated relative seed intake (see The quantitative component of disperser effectiveness) to determine the number of seeds defecated in each GRT interval. The dispersal distance for these seeds was randomly selected from the average displacement distance from origin (defined as the first location of the day) calculated for the corresponding time interval for each individual over all tracking days (see Quality of deposition). For the first time interval only (< 15 min), distance was randomly selected from the LRF data, based on tracking sessions shorter than 15 min (excluding three longer sessions for grackles and two for bulbuls); the LRF data are considerably more accurate than the radio telemetry data for short movements. Finally, the dispersal curve was produced by clustering dispersal distances of seeds into 100 m intervals. The entire procedure was repeated for 1000 iterations per species.

## RESULTS

### The quantitative component of disperser effectiveness

Bird feeding visits to *Ochradenus* shrubs were very common events but since only four of > 200 shrubs were video-monitored each day, only 41 visits (13 by grackles and 28 by bulbuls) were documented during the 322 h of observation. The daily (c. 7 h of observation) visit rate was  $0.68 \pm 0.51$  and  $1.47 \pm 0.84$  visits shrub<sup>-1</sup> day<sup>-1</sup> for grackles and bulbuls, respectively (Fig. 2a). Because days with no visits for the video-monitored shrubs were common, and since both bird species had identical exposure time to the video cameras, we used the exact binomial test to examine whether the visits divide equally between species, revealing that bulbuls are significantly more frequent visitors than grackles [ $X \sim \text{Binomial}(n = 41, p = 0.5)$ ,  $P = 0.027$ ], where  $P$  is the corresponding cumulative binomial distribution, i.e. the two-tailed probability to observe 13 or less visits by grackles among 41 total visits. In contrast, grackle visits were roughly three times longer than those of bulbuls ( $3 : 32 \pm 1 : 04$  vs.  $00 : 54 \pm 00 : 08$  min,  $t_{1.2} = 2.27$ ,  $P = 0.04$ ; Fig. 2b), and resulted in more fruit removed per visit, although this latter trend was insignificant ( $37.4 \pm 13.4$  vs.  $10.5 \pm 2.1$  fruit per visit,  $t_{8.3} = 1.98$ ,  $P = 0.08$ ; Fig. 2c). The fruit consumption rate of the grackles during a visit was slightly lower than that of the bulbuls ( $8.4 \pm 2.0$  vs.  $12.0 \pm 0.9$  fruit min<sup>-1</sup>, respectively), but not significantly so ( $t_{11.8} = 1.66$ ,  $P = 0.12$ ). Overall, the daily fruit consumption per shrub was similar for both species ( $7.3 \pm 6.7$  vs.  $5.9 \pm 4.4$  fruit shrub<sup>-1</sup> day<sup>-1</sup>,  $t_{18.9} = 0.17$ ,  $P = 0.86$ ; Fig. 2d).



**Figure 2** Quantity of dispersal and quality of treatment provided to *Ochradenus* by the two avian dispersers: grackles (black) and bulbuls (grey). (a) Daily visit frequency to fruit-bearing *Ochradenus* shrubs. Each day is represented by approximately 7 h of observations. (b) Duration of visits upon fruit-bearing *Ochradenus* shrubs. (c) Fruit removal rate during visits in fruit-bearing *Ochradenus* shrubs. (d) Daily fruit removal rate. (e) Cumulative proportion of defecated seeds as a function of gut retention time (GRT). (f) Effect of passage in bird's digestive tract on seed germination. Shown here is the net effect compared to two types of controls: seeds within intact fruit (Control 1) and seeds manually separated from fruit pulp (Control 2). Error bars indicate  $\pm$  SE. \* $P < 0.05$ .

## The qualitative component of disperser effectiveness

### *Quality of treatment – gut passage and germination experiments*

Gut retention time of grackles was much longer than that of bulbuls (mean  $\pm$  SE:  $135.1 \pm 14.1$  vs.  $34.7 \pm 1.5$  min,  $t_{8,1} = 7.8$ ,  $P < 0.0001$ , maximum  $\pm$  SE:  $328.3 \pm 12.6$  vs.  $91.5 \pm 7.3$  min,  $t_{10,4} = 17.4$ ,  $P < 0.0001$ , respectively; Fig. 2e). Individual birds (within species) did not differ in their gut passage effect on the proportion of germination (one-way ANOVA,  $F_{8,23} = 0.53$ ,  $P = 0.82$  for grackles,  $F_{6,20} = 1.45$ ,  $P = 0.272$  for bulbuls), but that proportion in controls differed significantly among trials (one-way ANOVA,  $F_{8,23} = 4.6$ ,  $P = 0.002$ ). This proportion was generally high, 12–62% and 68–88% for Control 1 (seeds within intact fruit) and 2 (manually separated seeds), respectively. Thus, to test the effect of passage through the digestive tract on germination, germination proportions of gut-treated seeds from each time interval, were compared to those of the *same* trial's control experiments. The mean net effect per species was averaged for each individual over

all trials and significance was evaluated by constructing 95% confidence intervals. Overall, 7024 seeds were included in these experiments.

Gut passage in both species had a similar effect on germination. Compared to control seeds within intact fruit (Control 1), passage in the digestive tract significantly improved germination by  $31.1 \pm 3.3\%$  for grackles and  $29.0 \pm 3.6\%$  for bulbuls (Fig. 2f). Compared to germination of manually separated seeds, passage through the digestive tract had a weak but significant effect in both species, decreasing germination by  $9.3 \pm 2.5\%$  and  $5.6 \pm 1.9\%$  ( $t_8 = 9.2$ ,  $P < 0.001$ ; Fig. 2f). The gut passage effect on germination was not correlated with GRT (i.e. treatment-control difference was independent of GRT), for both species ( $r^2 = 0.11$ ,  $P = 0.19$ ).

### *Quality of deposition*

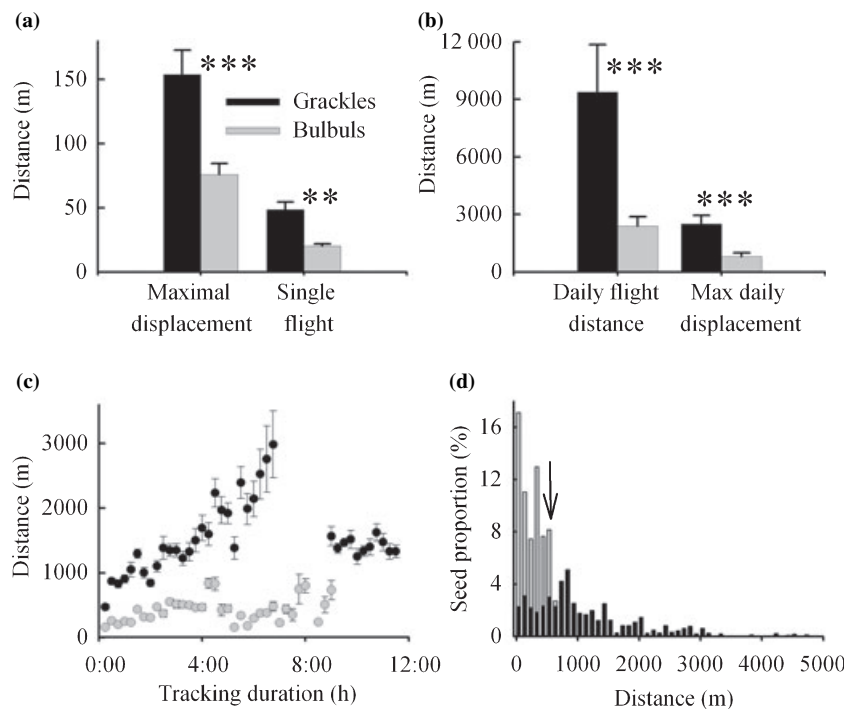
A total of 1153 positions (52 sessions) were acquired for grackles and 2230 positions (112 sessions) for bulbuls. Session duration ( $5 : 26 \pm 0 : 43$  and  $5 : 12 \pm 0 : 27$  min,

respectively) was evenly distributed between species (Kolmogorov–Smirnov  $Z = 0.662$ ,  $P = 0.773$ ). Flight distance was calculated as the aerial distance between successive positions, excluding static ( $< 2$  m difference) successive positions to avoid underestimation or bias. Mean flight distance of grackles was twice as large as that of bulbuls ( $48.5 \pm 5.9$  vs.  $20.2 \pm 1.7$  m, Mann–Whitney  $U$ -test,  $Z = -4.13$ ,  $P < 0.001$ ; Fig. 3a). Session displacement distance (distance from a session's first position) was also longer for grackles than for bulbuls, with mean maximal distances of  $153.9 \pm 18.9$  and  $75.0 \pm 8.3$  m per session, respectively ( $Z = -4.31$ ,  $P < 0.001$ ; Fig. 3a). Both species were selective in their choice of microhabitats, avoiding the open areas and favouring shaded microhabitats such as acacia trees within the wadis (Spiegel 2006; see Discussion).

Grackles performed significantly longer daily flights than bulbuls ( $9.38 \pm 2.47$  vs.  $2.39 \pm 0.47$  km day<sup>-1</sup>; max. daily flight distance  $> 20$  vs.  $< 5$  km,  $t_{9,9} = 8.39$ ,  $P < 0.0001$ ; Fig. 3b). Position accuracy is estimated by constructing

error ellipses of 95% CI ( $0.90 \pm 0.24$  and  $0.14 \pm 0.03$  km<sup>2</sup>, respectively) using a Maximum Likelihood Estimator (MLE; LOCATEIII software, Nams 2005) for positions acquired by three receivers ( $n = 100$  and  $n = 120$ , respectively). The estimated home range of grackles is considerably larger than that of bulbuls ( $1142 \pm 283$  vs.  $66 \pm 21$  ha, respectively, Mann–Whitney  $U$ -test,  $Z = 3.46$ ,  $P < 0.001$ ).

The first recorded location of the day was defined as the site of origin (usually  $< 2.5$  h after sunrise). The maximal daily displacement for the grackles was significantly longer than that of the bulbuls ( $2491 \pm 463$  vs.  $802 \pm 189$  m,  $t_{11,8} = 6.03$ ,  $P < 0.0001$ ; Fig. 3b). Mean displacement distance from the origin was calculated for each 15-min interval (Fig. 3c), excluding intervals with data from  $< 4$  different individuals. Grackle displacement distance increased nearly constantly with tracking duration, peaking at  $\approx 3000$  m after 7 h (900 m after 4 h for bulbuls), decreasing in longer tracking periods as the birds returned to their regular roosting sites.



**Figure 3** Movement patterns of the two avian dispersers, grackles (black) and bulbuls (grey), on two spatial scales and the dispersal curve they generate for *Ochradenus* seeds. (a) Small-scale movements measured using a laser range finder: maximal displacement distance during a tracking session, and length of a single flight. (b) Large-scale movement measured using radio-telemetry tracking: daily flight distance travelled by each species and the mean of maximal daily displacement distance (distance from origin, defined as first location of the day). (c) Displacement distance as a function of tracking duration, calculated for 15-min time intervals. (d) Dispersal curve of *Ochradenus* seeds dispersed by grackles (black) and bulbuls (grey), based on a simple mechanistic model combining the observed relative quantities of removed fruit, gut retention times and the distribution of displacement distances. The arrow represents the distance at which the two species switch roles: bulbuls disperse the majority of seeds in each distance class for shorter distances, while grackles are responsible for most of the seeds dispersed to longer distances. Error bars indicate  $\pm$  SE. \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ .

## Dispersal curves

We used a simple mechanistic model incorporating both small- and large-scale frugivore movements to predict bird-generated dispersal curves of *Ochradenus* seeds (Fig. 3d). We fitted a battery of probability density functions (PDFs) to the predicted dispersal curves generated by grackles, bulbuls and both, using Matlab 'dfittool' module. Among the PDFs tested, the Weibull distribution gave better fit (lowest negative log-likelihood) than the negative exponential, the gamma and the lognormal. The dispersal curves generated by the two species differed significantly in both the shape and the scale parameters of the fitted Weibull distribution (Table 1). The mean dispersal distance was considerably larger for the grackles than for the bulbuls ( $1168 \pm 840$  vs.  $303 \pm 176$  m, maximum 4800 and 900 m, respectively). Thus, *Ochradenus* seeds consumed by grackles have much higher probability to be dispersed over long distances compared to seeds consumed by bulbuls. Less than a fifth (*c.* 17%) of the seeds is predicted to be dispersed by the two species within 100 m from the mother plant, most of them (86%) by bulbuls (Fig. 3d). While bulbuls are responsible for most of the seed dispersal to shorter distances than 500 m, grackles are almost exclusively responsible for dispersal above 600 m and up to 4800 m.

## DISCUSSION

Grackles and bulbuls effectively disperse similar quantities of *Ochradenus* seeds and likewise improve seed germination. Nevertheless, as predicted from differences in their body size, they differ significantly in their home range, movement pattern and seed retention time in the digestive tract, consequently dispersing *Ochradenus* seeds to different range of distances. Thus, the difference in seed dispersal distances is the most significant component of disperser effectiveness over which the two species vary. This difference suggests that the two species provide complementary dispersal service to the plant. The bulbuls are the major dispersers at the scale of a few hundred meters within the local habitat (the wadi),

and thus are the major drivers of most local populations' dynamics. The grackles, however, are efficient LDD vectors capable for connecting the otherwise-isolated populations in neighbouring wadis. Differences in seed dispersal distances among animal dispersers have been demonstrated in several studies (e.g. Jordano *et al.* 2007), but not in the context of disperser effectiveness. We suggest that distance-dependent disperser effectiveness is a general phenomenon likely to occur in many other ecosystems as well, and therefore call for explicit investigation of dispersal distance in disperser effectiveness studies.

## The quantitative components of disperser effectiveness

The feeding rate we quantified for both species, about 10 fruit  $\text{min}^{-1}$  during visits, is comparable to that of other Pycnonotidae species (*Andropadus latirostris* and *A. tepbolenus*; Graham *et al.* 1995) and of cedar waxwing and American robin, birds of similar size (Chavez-Ramirez & Slack 1994). Although feeding rates show low variability, differences in visit duration and frequency can still vary fruit consumption. Both duration and frequency are context-dependent and affected by the spatial arrangement of resources and population sizes (Schupp 1993; Chavez-Ramirez & Slack 1994; Jordano & Schupp 2000).

The longer visits of the larger grackles correspond to the predicted general tendency of larger species to consume more food per visit (Jordano 1982; Jordano & Schupp 2000), although the difference found in the amount of consumed fruit per visit was only marginally significant. Bulbuls' visit frequency was significantly higher, either due to larger populations in the study site or due to larger dependence on *Ochradenus* fruit in their diet, compared to grackles. Although no exact estimation of population size for both species is available, we tend to favour the latter explanation for two reasons: First, bulbuls are known as almost obligatory frugivores while grackles are omnivores and fruits constitute a smaller portion of their diet (Cramp 1988). Second, the much smaller home range of the bulbuls (*c.* 70 vs. *c.* 1100 ha) probably amplifies scarcity of

**Table 1** Fitting of a Weibull probability density function to dispersal curves generated by a simple mechanistic model and calculated separately for each of the two avian frugivores (grackles and bulbuls), and for both species together

Species	Weibull parameters (confidence bounds)*		Median (confidence bounds)*	Mean $\pm$ SD dispersal distance (m)	Negative log likelihood ( $\times 10^7$ )	$R^2$
	Scale	Shape				
Grackles	1283.7 (1273.8–1293.8)	1.41 (1.39–1.42)	989 (980–999)	$1168 \pm 840$	7.97766	0.78
Bulbuls	340.8 (338.7–342.9)	1.78 (1.76–1.79)	277 (275–279)	$303 \pm 176$	6.50924	0.76
Both species	755.4 (747.6–763.3)	1.06 (1.06–1.07)	536 (529–543)	$736 \pm 689$	7.59496	0.87

All dispersal curves are significantly different from each other in values of the scale and shape parameters ( $P < 0.001$ ).

\*99.9% confidence bounds.

alternative food sources and their reliance on the year-round available *Ochradenus* fruit as the main source (Wolfe & Shmida 1997).

The opposing trends of longer visits by grackles vs. more frequent visits by bulbuls are comparable to those found by Jordano (1982). The resulting similarity in fruit removal rates in the order of 10 fruit shrub<sup>-1</sup> day<sup>-1</sup> corresponds to the independent observation of similar proportions of time spent by the two species on *Ochradenus* during the LRF tracking sessions ( $31 \pm 6\%$  for grackles and  $34 \pm 4\%$  for bulbuls). Overall, we conclude that the two species do not differ significantly in the number of seeds they consume and disperse in the study system.

### The qualitative components of disperser effectiveness

#### *Quality of treatment*

Regardless of the major differences in GRT, the two bird species had very similar effects on the germination of *Ochradenus* seeds they digested. On one hand, seed digestion decreased germination by *c.* 5–10% compared to manually separated seeds, presumably due to seed coat erosion (Ladley & Kelly 1996; Traveset & Verdu 2002). On the other hand, digestion increased germination by *c.* 30% compared to seeds within intact fruit, most likely due to the removal of physical and chemical germination barriers or to better water availability for the seed, associated with pulp removal (Ladley & Kelly 1996; Traveset & Verdu 2002). Clearly, the intact fruit control reflects the natural situation of non-digested seeds more faithfully; thus, digestion by each of these two bird species entails a strong positive effect on germination of *Ochradenus* seeds. The high germination proportion and the seed miniature size (*c.* 2 mm diameter) imply that seed dormancy is not common in this species.

#### *Quality of deposition*

The patterns of frugivore foraging movements can also strongly impact seed dispersion patterns and consequently influence population spatial structure (Chavez-Ramirez & Slack 1994; Schupp & Fuentes 1995; Jordano *et al.* 2007). In the arid environment of our study site, seed arrival at a suitable site, where the harsh abiotic conditions are mitigated, is critically important (Tewksbury & Lloyd 2001). In addition to their positive effects on seed germination, both species minimize the time spent in the unsuitable areas between wadis suggesting minimal seed loss in the hostile matrix. Furthermore, a disproportionate amount of seeds is transferred to presumably favourable establishment microsites within the wadi, mostly beneath woody plants used for perching (Altstein 2005; Spiegel 2006, O. Spiegel & R. Nathan, unpublished data).

### Disperser body size and seed dispersal distance

Despite the high similarity in the quantity and quality of dispersal, the two bird species differ markedly in the scale over which they disperse *Ochradenus* seeds, as expected from the differences in their body size. Two entirely independent data sets on movement patterns of the two avian dispersers show agreement among two quantified spatial scales, where the larger grackles perform much longer flights than bulbuls both at the local, and even more, at the regional scale. In addition, seeds are retained in their gut for much longer periods. Larger animals tend to cover greater areas in their daily foraging bouts (Jetz *et al.* 2004; Makarieva *et al.* 2005), and retain seeds for longer periods (Karasov 1990; Murphy *et al.* 1993), thus are often more efficient LDD vectors than smaller animals (Westcott & Graham 2000; Jordano *et al.* 2007). For example, longer dispersal distances were estimated for the larger (1000 g) great-blue turaco having a 50-fold greater home range than two smaller (250 g) turaco species (Sun *et al.* 1997), and for the larger among 11 waterfowl species for which body mass (ranging between 0.3 and 10.7 kg) is positively correlated with seed retention time (data from Clausen *et al.* 2002).

Interestingly, the home range size of both grackles and bulbuls is considerably greater than that expected from universal allometric relationships published in the literature (Makarieva *et al.* 2005; Price 2006). Additionally, the observed 15-fold difference in home range size between grackles and bulbuls is much greater than the expected fourfold difference expected from their allometric ratio (Makarieva *et al.* 2005). The scarcity of available resources within wadis in hot deserts may explain the relatively large home ranges of both species, and the wide dry habitat between wadis may explain the exceptionally large home range of grackles. The inter-wadis movements measured here for the grackles are essentially similar to inter-patch movements performed by much larger frugivores in other fragmented or patchily distributed environments (Fragoso 1997; Holbrook & Smith 2000; Price 2006). Consequently, our estimated dispersal distances are comparable to those estimated for hornbills (1038–1431 g; Holbrook & Smith 2000), and are considerably longer than those estimated for turacos (250–1000 g; Sun *et al.* 1997). We emphasize that such differences must be examined in relation to the scale of resource patchiness in the study system (see following section).

We also note that comparisons between mechanistically derived dispersal curves and those estimated by inverse modelling from seed-trap data (e.g. Clark *et al.* 2005) are problematic, because inverse modelling do not capture well the properties of the tail given scarcity of LDD data (Nathan & Muller-Landau 2000). Nevertheless, future



quantitative comparisons among mechanistic models can be executed by fitting a PDF to the mechanistically-derived dispersal curve, as shown in this study (Table 1).

### Distance-dependent disperser effectiveness is widespread and important

Schupp (1993) and subsequent investigators emphasized the importance of two quantitative (number of visits and number of seeds dispersed per visit) and two qualitative (quality of treatment and quality of deposition) components of disperser effectiveness. According to this common implementation of the disperser effectiveness concept, the two dispersers we have studied contribute equally to *Ochradenus* fitness. Yet, by considering seed dispersal distances we found a striking difference in the dispersal service they provide to the plant, emphasizing the important role of LDD in heterogeneous environments (Chambers *et al.* 1999; Cain *et al.* 2000; Nathan & Muller-Landau 2000; Levin *et al.* 2003; Nathan 2006).

Differences in the scales of movement of frugivores in relation to their resources and, consequently, remarkable differences in seed dispersal distances among vectors dispersing the same plant species, have been demonstrated in several systems (Kollmann 2000; García & Ortiz-Pulido 2004; Tellería *et al.* 2005; Jordano *et al.* 2007; Nathan 2007). Some examples include corvids and scatter-hoardings rodents (Chambers *et al.* 1999), and endozoochorous (Myers *et al.* 2004) and epizoochorous (Mouissie *et al.* 2005) herbivores. These studies examined dispersal distance *per se*, without addressing explicitly questions of disperser effectiveness. Other studies addressed disperser effectiveness in heterogeneous environments, but without explicitly considering dispersal distance or spatial-scale effects (Loiselle & Blake 1999; Santos *et al.* 1999; Jordano & Schupp 2000; Calviño-Cancela 2002; Hollander & Vander Wall 2004; Martins 2006). Nevertheless, distance-dependent disperser effectiveness is very likely to occur in many of these cases; for instance, differences between seagulls, rabbits and blackbirds (Calviño-Cancela 2002), between the 170 g white-winged dove and the 20 g lesser long-nosed bat (Godínez-Alvarez *et al.* 2002), and among different passerines (Loiselle & Blake 1999).

The key finding of this study, that the two bird species switch roles as a function of spatial scale and thus provide complementary dispersal service to the plant, helps elucidate the importance of distance-dependent disperser effectiveness. Bulbuls disperse most of the seeds within the local habitat (the wadi) and thus play a key role in shaping the local population dynamics of this species, and probably other fleshy-fruited plants as well (e.g. *Capparis* spp.). Grackles disperse some *Ochradenus* seeds locally, but play an exclusive role in dispersing seeds between wadis, uniquely

contributing to plant fitness in the long-term, especially if populations are at risk of local extinction due to disturbances or catastrophes (e.g. floods).

Future investigations of distance-dependent disperser effectiveness may reveal less substantial differences in dispersal distances than those reported here. However, whether or not the difference found here is extreme is less important than the question if such differences correspond to the scale at which the main resources are distributed in the study ecosystem. In other words, the main challenge is to identify the critical breakpoint(s) in the spatial scale over which dispersers – potentially differing in a predictable way (e.g. body size) – vary in their contribution to plant fitness. In our arid ecosystem, a sharp boundary exists between the sparsely vegetated local habitat (the wadi) and the hostile matrix between neighbouring wadis (Fig. 1). Wadis are typically few hundred metres wide and few kilometres apart (see Methods). Thus, the range of distances over which bulbuls and grackles disperse *Ochradenus* seeds, with a breakpoint at approximately 600 m, corresponds very well to the local (within wadi) vs. regional (between wadis) patchiness of this ecosystem.

Incorporating dispersal-distance effects into the traditional disperser effectiveness framework would provide more comprehensive and realistic evaluation of the relative importance of different dispersers. In particular, the concept should be revised to integrate both short- (*sensu stricto*: number of seedlings in the following generation) and long-term (*sensu lato*: the probability of population survival and spread) components of fitness. Investigation of distance-dependent disperser effectiveness should provide better understanding of plant–frugivore interactions and their underlying ecological and evolutionary processes and new insights for conservation, e.g. assessing the consequence of disperser extinction for populations of a key species such as *Ochradenus* in a disturbance-prone ecosystem such as seasonally flooded wadis.

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