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Frugivory in European Laurel: how extinct seed dispersers have been substituted

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Capsule Extinction of ancient frugivores during the Quaternary has led to a depauperated seed disperser community for *Laurus nobilis* and a tight mutualism between the plant and the Blackbird *Turdus merula*.
Aims To describe a present-day frugivore assemblage of natural Laurel populations in southern Spain.
Methods Eight fruiting trees of different size were monitored with binoculars during 52 hours spread across one ripening season, and the identity and behaviour of foraging birds were recorded. Additional point counts were used to record the avifauna of the surroundings.
Results Despite a diverse frugivore community being present, Laurel fruits are almost exclusively (99%) consumed by Blackbird and rarely (1%) by Blackcap *Sylvia atricapilla*. Blackbirds concentrate at fruiting trees and individuals may remain there for several days. Birds usually forage in small groups and return at intervals of 12–14 minutes.
Conclusion The Blackbird population of the study area forages extensively on the energy-rich Laurel fruits, while the plants depend exclusively on this bird species for seed dispersal. Consequences of the depauperate frugivore community and the tight mutualism between Blackbirds and Laurels on plant recruitment and conservation are discussed.

The European Laurel *Laurus nobilis* is probably the most emblematic tree of the subtropical so-called 'lauroid forests' that covered large parts of Europe in the Tertiary (Mai 1989). As most members of the Lauraceae, it produces relatively large, heavy-seeded and lipid-rich drupes and relies on medium- or large-sized frugivorous birds for seed dispersal. During the Quaternary glaciations many of these dispersers became extinct (Blondel & Mourer-Chauvire 1998), while the formerly widespread lauroid forest vegetation was pushed back to small refugium areas in the southern Mediterranean Basin and on the Macaronesian Islands (Mai 1989). Remnants of the original seed disperser assemblages have only been conserved on the East Atlantic archipelagos, where three species of endemic pigeons (*Columba trocaz*, *C. junoniae* and *C. bollii*) forage extensively on fruits of *Laurus azorica* and other species of the remaining laurel forests and are assumed to be their main dispersers (Cramp 1985, Snow & Snow 1988, Martín *et al.* 2000). The present-day frugivore community of European Laurel (hereafter Laurel) remains virtually unknown (but see Snow & Snow 1988, Debussche & Isenmann 1989).

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I report on the frugivore assemblage of natural Laurel populations located in southern Spain and address the following questions. (1) Are Laurel fruits regularly consumed by birds and by which species? (2) How do frugivores behave? (3) What are the consequences of the behaviour of present-day frugivores on the Laurel's seed dispersal?

Although the natural distribution range of Laurel is largely restricted to southeastern Europe, it has been commonly cultivated and is today growing across the Mediterranean Basin and parts of Atlantic Europe. Autochtonous populations have also survived on the southwestern Iberian Peninsula. They grow scattered in riparian forests of the mountain ranges in the Straits of Gibraltar region, a refugium of numerous Tertiary relict plant species (Ojeda *et al.* 2000). Female trees can produce a few thousand fruits (size 14.8 × 12.2 mm, weight 1234 mg, seed weight 698 mg; Herrera 1987). These ripen from mid-September until early November and may remain on the tree ripe for approximately four weeks (A. Hampe unpubl. data).

METHODS

Eight fruiting trees located at distances between 150 m

and 2 km and with crop sizes between 150 and 5200 fruits were monitored in the Aljibe Mountain Range, 40 km north-northwest of Gibraltar (36°30′N, 5°35′W, Andalusia, southern Spain). Each tree was observed every 7–10 days throughout its ripening season (total period 20 September to 17 November 2001). Observations lasted two hours and were spread over the day (8:30–18:30 hours).

The order of focal trees monitored through a given day was determined at random to preclude biases from timely changes in birds' foraging activity. Observations were made using binoculars from a cover located between 20 and 40 m away from the focal tree. Before monitoring, I counted the number of unripe and ripe fruits using binoculars. The local avifauna was recorded during a 10-min point count.

Each bird observation within a radius of 50 m was assigned either to the habitat of Laurel (riparian forest) or the surrounding vegetation, made up mostly of oak forest (*Quercus suber* and *Q. canariensis*) or sclerophyllous scrub (see Hampe & Bairlein 2000 for details). Other bird species observed in the area during the two-hour tree monitoring were also recorded. When a focal tree was visited by fruit-foraging birds, I recorded whenever possible the species, sex, individual plumage characteristics, arrival time, duration of the foraging bout, number of fruits ingested, and presence of other frugivores in the tree.

Table 2. Foraging behaviour of the two species observed consuming Laurel fruits (mean ± 1 sd, *n* given in parentheses).

	Blackbird	Blackcap
Total foraging bouts	171	6
Duration (s)	117 ± 86 (104)	55 ± 49 (5)
Ingested fruits per bout	3.5 ± 1.7 (67)	1.0 ± 0.0 (6)
Bouts in association with other birds (%)	67.8	83.3

RESULTS

I recorded 20 bird species in the study area, of which 15 were regular frugivores (Table 1). Only Blackbirds *Turdus merula* and Blackcaps *Sylvia atricapilla* consumed Laurel fruits. Blackbirds accounted for 96.6% of the recorded foraging bouts and 99.0% of the consumed fruits (calculated as the number of foraging bouts multiplied by the mean fruit number ingested per bout; see Table 2).

Individual trees received between 0.0 (two plants) and 15.5 ± 9.2 (mean ± sd) foraging bouts during a two-hour observation period. The focal tree's fruit crop size

Table 1. Avifauna recorded in the study area. For each species are shown: (i) frugivore status according to Herrera (1984), Debussche *et al.* (1989), Jordano & Schupp (2000) and Hampe (2001); (ii) proportion of two-hour monitoring periods with the species present in the surroundings; (iii) total number of records during 10-minute point counts (n = 313); (iv) proportion of records within the Laurel habitat (i.e. riparian forest); and (v) number of recorded foraging bouts.

Species	Frugivore status	Presence monitoring (%)	Records point counts	Records Laurel habitat (%)	Foraging bouts
Sparrowhawk *Accipiter nisus*	NF	4	0	–	0
Long-tailed Tit *Aegithalos caudatus*	PC	31	3	67	0
Short-toed Treecreeper *Certhia brachydactyla*	NF	81	19	21	0
Wood Pigeon *Columba palumbus*	SD	4	0	–	0
Great Spotted Woodpecker *Dendrocopos major*	SP SD	46	4	0	0
Robin *Erithacus rubecula*	SD	100	123	75	0
Chaffinch *Fringilla coelebs*	PC SP	46	13	17	0
Jay *Garrulus glandarius*	PC SD	54	4	0	0
Spotted Flycatcher *Muscicapa striata*	SD	4	0	–	0
Blue Tit *Parus caeruleus*	PC SD	85	17	56	0
Great Tit *Parus major*	PC	27	5	0	0
Crested Tit *Parus cristatus*	PC	62	7	0	0
Iberian Chiffchaff *Phylloscopus brehmii*	NF	23	3	0	0
Firecrest *Regulus ignicapillus*	NF	96	26	23	0
Nuthatch *Sitta europaea*	SP PC SD	81	17	13	0
Blackcap *Sylvia atricapilla*	SD	88	41	92	6
Wren *Troglodytes troglodytes*	NF	85	10	90	0
Blackbird *Turdus merula*	SD	69	20	80	171
Song Thrush *Turdus philomelos*	SD	12	1	0	0
Mistle Thrush *Turdus viscivorus*	SD	4	0	–	0

SD, seed disperser; SP, seed predator; PC, pulp consumer; NF, non-frugivore; –, no record.

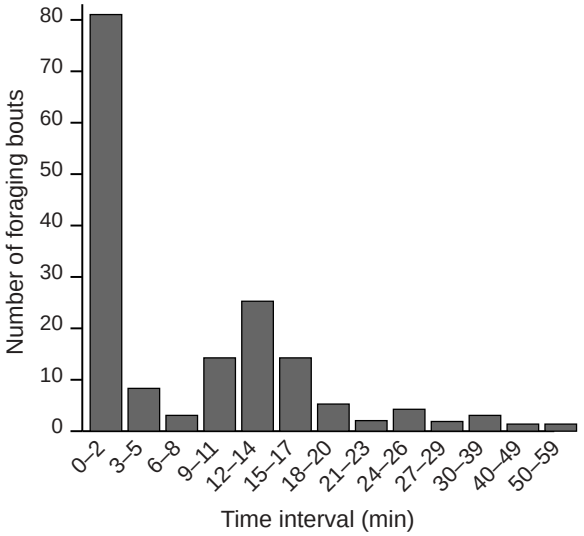

Figure 1. Time intervals between subsequent Blackbird foraging bouts at focal trees recorded during two-hour monitoring periods. Individuals were not distinguished, so shown intervals may refer either to repeated visits by the same bird or sequential visits by two different birds.

was correlated with the number of observed foraging bouts per monitoring unit (Spearman's: $r_s = 0.83$, $n = 8$, $P = 0.01$) and the abundance of Blackbirds in the vicinity ($r_s = 0.73$, $n = 8$, $P = 0.04$).

Birds often foraged in association with other individuals (Table 2). The time intervals between subsequent Blackbird foraging visits showed a bimodal distribution with a strong peak at 0–2 min and a secondary one at 12–14 min (Fig. 1).

DISCUSSION

Frugivore community

In terms of species diversity, the Laurel's assumed former seed disperser community has been poorly substituted. Today only a single bird species makes regular use of the abundant, high-quality food source provided by Laurel fruits. Such a strong limitation of frugivore communities is uncommon and usually restricted to species-poor habitats like alpine regions (Herrera 1995).

The riparian forests and their surroundings bear a diverse and abundant frugivorous bird community, and fruits of *Frangula alnus*, a species sharing the same habitat, are consumed by at least 12 bird species (Hampe 2001). However, most recorded frugivores are small-sized and unable to swallow the large Laurel fruits (Herrera 1984). Larger species (*Columba palumbus*, *Garrulus glandarius*, *Dendrocopos major* and *Turdus* spp.) are scarce, as they occur mostly outside the dense riparian vegetation and some of them prefer to feed on acorns, which are abundant during the Laurel's ripening season (A. Hampe pers. obs.).

As a result, Laurels receive markedly less frugivore visits than *Frangula alnus* trees (Hampe 2001) and may even experience no fruit removal at all, as was observed (and confirmed by fruit counts) at two of the eight trees monitored during this study. In the same way, there was a surprising absence of pulp-pecking birds despite the very high nutritional value of their pulp (lipid content 54.3 % according to Herrera 1987).

Frugivore behaviour

Blackbirds tended to concentrate around fruiting Laurels during the ripening season, and large trees were regularly visited by single individuals or small groups of up to four birds. Observations of two recognizable individuals (one partially albinistic and one with parts of the head feathers missing), as well as the constant sex ratios of foraging Blackbird groups recorded on repeated observations, indicate that foraging bouts during the two-hour monitoring periods were made by the same individuals. Moreover, birds may remain close to trees during several days, with some evidence of birds staying for at least two weeks around the same tree.

The distribution of time intervals between foraging bouts suggests two distinct aspects of Blackbirds' foraging behaviour. The first peak at 0–2 min indicates that birds synchronize their bouts and forage simultaneously. The second peak at 12–14 min suggests that this is about the time birds need for fruit processing and seed regurgitation (seeds are too large for gut passage), before they return for subsequent foraging bouts (see Sorensen 1984 for experimental data on fruit digestion by Blackbirds). Very few studies have reported fruit processing times of frugivorous birds in the field (Yumoto 1999), although the timing of seed retention and delivery plays an important role for the spatial pattern of bird-generated seed rains and subsequent plant recruitment processes (Jordano 2000, Jordano & Schupp 2000, Wenny 2000).

In conclusion, Blackbirds appear to forage heavily on Laurel fruits in the study area. Surprisingly, they are apparently not affected by the large amount of diverse secondary compounds (such as tannins, terpenes and other phenolic compounds) they ingest with the fruit pulp (Snow & Snow 1988; see Jordano 2000 for a review of contrary cases). On the other hand, the fruit consumption rates suggest that a few resident

Blackbirds are able to deplete an entire Laurel fruit crop over its ripening season of 4–6 weeks. In this sense, Blackbirds may therefore be considered efficient substitutes for Tertiary frugivores.

Ecological and evolutionary implications

I report an unusually depauperate and direct fruit–frugivore mutualism (Herrera 1995), which is ultimately a consequence of the extinction of other dispersers. Increasing evidence suggests that depauperate frugivore communities may negatively affect the seed dispersal and recruitment success of plant populations (Santos & Tellería 1994, Bleher & Böhning-Gaese 2001, McKonkey & Drake 2002). If seeds are dispersed by few or a single species, many of them may be delivered to certain microhabitats, while other sites receive few or no seeds and are thus lost for the recruitment (Jordano & Schupp 2000, Godoy & Jordano 2001).

The observed high site fidelity of Blackbirds suggests that Laurel seeds are rarely dispersed more than a few dozen metres from the mother tree. Blackbirds thus scarcely promote genetic interchanges between remote Laurel populations, contrary to Mistle Thrushes *Turdus viscivorus* in southeastern Spanish *Prunus mahaleb* metapopulations (Godoy & Jordano 2001). A reduction in Blackbird abundance (e.g. due to hunting), as well as a switch to other diets or other habitats (e.g. due to changing land management in the surroundings) might further reduce the yet limited seed dispersal within and among the small, isolated Laurel populations (cf. Steadman 1997, McKonkey & Drake 2002). Therefore, the local conservation of the apparently 'ubiquitous' Blackbird may play a key role for the long-term survival of natural Laurel populations in their southern Iberian refugium areas.

From an evolutionary perspective, the present case argues against adaptationist views of fruit–frugivore mutualisms (Herrera 1995). Laurels might presumably reach a considerable fitness gain by producing smaller fruits which could also be ingested and dispersed by small-sized frugivores. However, despite the long time populations have presumably persisted in the study area they have not produced fruits small enough for small-sized dispersers, and they are at present experiencing reduced recruitment (A. Hampe unpubl. data) partly due to this 'adjustment failure'.

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