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Macrogeographic variations in food choice of mainland citril finches *Carduelis [citrinella] citrinella* versus insular Corsican (citril) finches *Carduelis [citrinella] corsicanus*

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Abstract We studied variations in diet composition in sub-populations of mainland citril finches *Carduelis [citrinella] citrinella* in European mountain chains, compared to closely related insular Corsican (citril) finches *Carduelis [citrinella] corsicanus* on several Mediterranean Islands with a special emphasis on key food plants used during the breeding period. We found that citril finch sub-populations of the Pre-Pyrenees and the Black Forest rely mostly on mountain pine and dandelion seeds as main food resources during the breeding season. In contrast, insular Corsican finches on the Mediterranean islands of Capraia and Corsica fed mainly on various herb species. Finches in Corsica fed predominantly on shepherd's purse, while birds from Capraia were choosing rosemary as their main food plant during the breeding period. These observations confirmed the previously expected difference in food choice between the two forms due to the observed increased niche breadth on Corsica. However, Corsican finches on Sardinia showed a food choice more similar to that of the citril finch populations, in that they fed predominantly on black pine seeds during breeding season. Thus we were not able to find clear behavioural differences in diet composition between all studied sub-populations of citril and Corsican finches. To conclude, food choice of both forms is highly adaptive and, in the different breeding areas, distinct key plants may be of special importance during the breeding season. The preference for these plants is likely to be linked to their abundance and their energetic and nutritional content.

Keywords *Carduelis citrinella* · *Carduelis corsicanus* · Citril finch · Corsican finch · Food choice · Insular versus mainland populations · Niche expansion

Introduction

Among European finches, citril finches *Carduelis [citrinella] citrinella* are the only ones to be restricted to a few mountain zones of western and south-western Europe above 800 m a.s.l. (Cramp and Perrins 1994; Baccetti and Märki 1997; Glutz von Blotzheim and Bauer 1997). As birds of the sub-alpine and mountainous zones, they are especially exposed to a mountainous climate with cold spells, rain storms and snow. Thus, they have to deal more with severe and sudden changes in their living conditions than other European finches (Newton 1967, 1985). Therefore, citril finches are forced to develop survival strategies especially adapted to their mountainous surrounding (Förchler and Kalko, in preparation). One of the most important adaptations is the optimal use of food resources to fulfil the requirements for successful breeding and nestling growth (Newton 1967).

Until recently, knowledge on the feeding ecology of citril finches was limited mostly to studies on diet composition after the breeding season (Sabel 1965; Mau 1980). During this time (July–September), citril finches feed on a great variety of seeds from grasses and herbs. Therefore, some authors classified the citril finch as a generally non-specialised, granivorous bird with preferences for grass seeds (Märki 1976; Cramp and Perrins 1994). However, preliminary data from citril finches in the northern Black Forest suggest a seasonally strong dependence on pine seeds, especially on the energy-rich seeds of the mountain pine *Pinus mugo* (Hölzinger and Dorka 1997; Glutz von Blotzheim and Bauer 1997; personal observations). These data were further supported by quantitative studies on citril finch diet in the Black Forest (Förchler 2001a) and in the Pre-Pyrenees (Borras et al. 2003) during the breeding season when

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citril finches feed temporarily on seeds of only a few plant species, e.g. mountain pines, dandelion *Taraxacum officinale* and common sorrel *Rumex acetosa*. Late onsets of winter regularly force the birds to 'migrate' from their breeding grounds to lower areas (refuge sites) where there are other food sources such as germander *Teucrium scorodonia* (Förschler 2001b).

The closely related sister-taxon Corsican (citril) finch *Carduelis [citrinella] corsicanus* occurs on a few mountainous Mediterranean islands, including Corsica, Sardinia, Elba, Capraia, and Gorgona (Arcamone 1993; Cramp and Perrins 1994; Baccetti and Märki 1997; Thibault 1983; Thibault and Bonaccorsi 1999; Lamberini 2000, 2002; Moltoni 1975). While citril finches are restricted to the sub-alpine and mountainous zone, Corsican finches exhibit a large niche expansion into Macchie habitats (Martin 1982, 1992; Blondel et al. 1988), which promotes a population expansion to lower elevations on Corsica (Thibault 1983; Blondel 1985; Blondel et al. 1988; Thibault and Bonaccorsi 1999). In contrast to citril finches, the diet of the closely related Corsican finches is virtually unknown, except for a few anecdotal observations mentioning grass seeds and Compositae seeds as main food sources (Marzocchi 1990; Thibault and Bonaccorsi 1999).

In a detailed comparative study on the breeding ecology of the two forms, we found variations in nest site and habitat selection, with Corsican finches preferring the low and dense tree heath *Erica arborea* as nesting plants instead of nearby available higher trees (especially pines), while citril finches were always found breeding in the predominant conifers (Pinaceae), mainly distinct pine species (Förschler and Kalko, in preparation). This behavioural change in Corsican finches additionally promotes the increased niche breadth on the islands (Blondel et al. 1988).

In a comparative analyses of blue tit *Parus caeruleus* populations, a significant difference in feeding ecology was found between a typical Mediterranean deciduous habitat on the mainland and a sclerophyllous habitat on the island of Corsica (Blondel et al. 1991). Blue tits of the islands showed a higher diversity for food items and preferred larger prey items during the breeding period than did birds on the mainland. A larger spectrum of occupied habitats linked to changes in feedings habits, involving a greater versatility or shifts in feeding behaviour, have also been noticed by many authors (Blondel 1985).

In line with these observations, we expected to find qualitative differences in feeding composition of mainland citril finches versus island Corsican finches as well, because of the notable differences in habitat choice between the two citril finch forms (Förschler and Kalko, in preparation), and taking into account the recommended classification of the insular Corsican finch as a separate species with its own evolutionary history due to the results of genetical analyses (Pasquet and Thibault 1997; Sangster 2000; Sangster et al. 2002).

To study the expected variations, we focussed our research on the food choice of citril and Corsican finches during the breeding season, because in this period only a few food plant species may supply the energetic needs for successful breeding (Förschler 2001a; Borrás et al. 2003; Valera et al. 2005). We expected to find typical key plants in the distinct areas. As study objects, we selected sub-populations of mainland citril finches in the Black Forest and the Catalanian Pre-Pyrenees, and sub-populations of insular Corsican finches in Sardinia, Corsica and Capraia.

Citril and Corsican finches have long been considered to belong to the genus *Serinus* (canaries) (Nicolai 1957; van den Elzen and Khoury 1999). However, according to the results of new molecular studies on canaries and goldfinches, citril finches have recently been reclassified within the genus *Carduelis* (goldfinches) (Arnaiz-Villena et al. 1998, 1999). Following this, Corsican finches have to be reclassified into the genus *Carduelis* as well. In our study we used the new classification of the former super-species *Serinus [citrinella]* as *Carduelis [citrinella]* (see also Helbig 2005).

Materials and methods

The feeding ecology of citril and Corsican finches was studied at five research areas during the nesting and breeding period. Study sites for citril finches included Mount Schliffkopf in the Northern Black Forest (1999) and Port del Comte mountain in the Catalanian Pre-Pyrenees (2002). Sites for Corsican finches encompassed the mountains of Niolo/Evisa in northern Corsica and the Massif de l'Ospedale in southern Corsica (2001), the small island of Capraia (2003) and Monte Limbara in northern Sardinia (2003). Here we visually assessed every feeding observation of finches in the months April–July during the breeding period. For each observation of foraging finches we noted plant species and the number of birds.

We followed Newton (1967) and quantified our observational data as follows: one record = one bird with one food source. If we detected, for example, a group of five citril finches feeding on mountain pine seeds, we counted five birds feeding on the food source mountain pine seeds = five records. For this analysis, we avoided taking into account the time spent on the use of the plant, because in some cases birds can be observed for hours in the surrounding of one food plant and those observations would have led to overestimations.

As an individual bird may react differently towards the presence of an observer, the results may be somewhat biased, but other studies have shown that this is of minor importance (Newton 1967). Citril and Corsican finches have very short flight distances and can be observed very easily during feeding (Sabel 1965; Mau 1980; personal observations). Thus, the observational data of feeding finches are representative of the real food choice of

the species. Furthermore, it has been demonstrated that observational field data of diet composition in finches coincides with results of gut and gullet analyses (Newton 1967; Borras et al. 2003).

As demonstrated in serins *Serinus serinus*, the diet of adults and their offspring is almost the same during the breeding season (Valera et al. 2005). So we may consider our data on the food choice of adult citril and Corsican finches to also be representative for their offspring.

Results

Mainland citril finches

Both populations of the citril finch, in the Catalanian Pre-Pyrenees as well as in the Black Forest, showed a strong preference for seeds of mountain pines in the 2 years of our study (Fig. 1, Table 1). Birds breeding in the northern Black Forest fed mainly on seeds of the mountain pine sub-species *rotundata* (52%) and birds of the Pre-Pyrenees on seeds of the mountain pine sub-species *uncinata* (64%). Seeds of the Scots pine *Pinus sylvestris* were of minor importance. Additionally, seeds of a few abundant herbs and grasses were also frequently eaten. Included in those, dandelion (Asteraceae) played a key role in both areas (Fig. 1, Table 1). In the Black Forest, we also observed an uptake of insects, especially aphids (Aphidina), as complementary food (Fig. 1, Table 1).

Insular Corsican finches

In northern Sardinia, diet composition during the breeding season in 2003 was similar to that of mainland citril finches. The majority of seeds taken by Corsican finches on Sardinia consisted of black pine *Pinus nigra* (42%). In addition, seeds of small herbs such as shepherd's purse *Capsella rubella* and some grass seeds were of importance. We also observed that ermine moths

(Parahyponomeutidae) in larval and pupal stage, that were locally highly abundant on tree heath *E. arborea*, added substantially to the nutrition (Fig. 1, Table 1).

In contrast to birds from the Black Forest, the Pyrenees and Sardinia, birds from Corsica and the island of Capraia hardly used any pine seeds during the breeding season in 2001 and 2003 (Fig. 1, Table 1). In Corsica, we observed a very high proportion of herb seeds in the food, mainly shepherd's purse, but also chickweed *Stellaria media*, mouse-ear *Cerastium fontanum* and whitlow grass *Erophila verna* (Fig. 1, Table 1). Birds from Capraia fed almost exclusively on buds and ovaries of rosemary *Rosmarinus officinalis* at the beginning of the breeding season (Fig. 1, Table 1).

Discussion

As expected, we found in all studied populations of citril and Corsican finches a limitation to a few key plants which were ingested predominantly during the breeding period. This selective feeding behaviour on a few plant species is generally considered to be rare among carduelid finches, which are described as more or less opportunistic (Newton 1967, 1985). However, a similar behaviour of food limitation to what we found for citril and Corsican finches has recently been described for serins (Valera et al. 2005).

The two selected study areas for sub-populations of mainland citril finches (Black Forest, Pre-Pyrenees) clearly revealed pine seeds as a dominant food source during the breeding season (see also Förschler 2001a; Borras et al. 2003). At the time when the finches selected their breeding sites and started nesting, citril finches in both areas fed almost exclusively on seeds of mountain pines. It is highly likely that citril finches always choose their breeding sites at places with good conifer seed resources (Förschler 2001a; Förschler et al. 2005). In consequence, we suppose that, generally, several conifer species, such as mountain pine, Scots pine and black pine, represent essential habitat elements at breeding

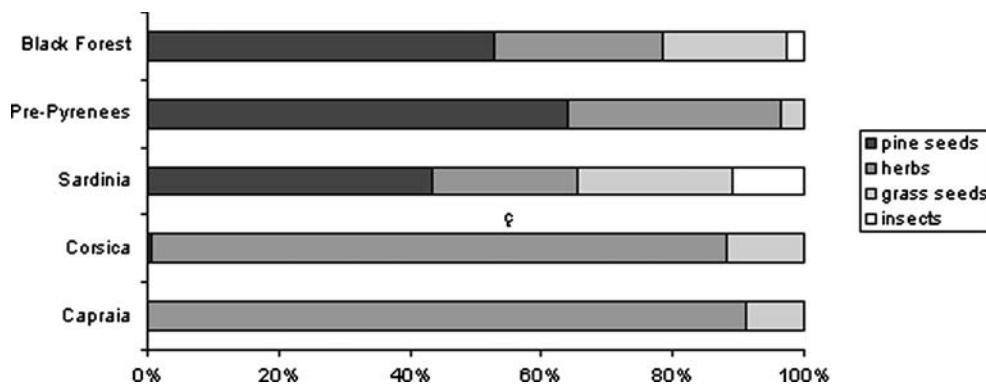


Fig. 1 Diet composition of citril finches *Carduelis [citrinella] citrinella* and Corsican finches *Carduelis [citrinella] corsicanus* in the distinct study sites. Black Forest, Mount Schliffkopf, April–July 1999, $n=522$ records; Catalanian Pre-Pyrenees, Port del

Comte, April–June 2002, $n=342$ records; Sardinia, Monte Limbara, April–June 2003, $n=584$ records; Corsica, Niolo and Massif de l'Ospedale, April–June 2001, $n=954$ records; Capraia, April–May 2003, $n=67$ records

Table 1 Food items of citril finches *Carduelis [citrinella] citrinella* and Corsican finches *Carduelis [citrinella] corsicanus* noted during breeding season in the distinct areas and their importance

Species	Family	Black Forest April–July 1999	Pre-Pyrenees April–June 2002	Northern Sardinia April–June 2003	Corsica April–June 2001	Capraia April–May 2003
<i>Bellis perennis</i>	Asteraceae				S	S
<i>Carlina macrocephala</i>	Asteraceae				S	
<i>Cirsium vulgare</i>	Asteraceae	S				
<i>Hyoseris radiata</i>	Asteraceae				S	
<i>Leontodon hispidus</i>	Asteraceae	S				
<i>Taraxacum officinale</i>	Asteraceae	D	D			
<i>Capsella bursa-pastoris</i>	Brassicaceae		S			
<i>Capsella rubella</i>	Brassicaceae			S	D	
<i>Erophila verna</i>	Brassicaceae	S	S		S	
<i>Cerastium fontanum</i>	Caryophyllaceae	S	S		S	
<i>Cerastium</i> sp.	Caryophyllaceae				S	
<i>Stellaria graminea</i>	Caryophyllaceae	S				
<i>Stellaria media</i>	Caryophyllaceae	S	S		S	
<i>Stellaria</i> sp.	Caryophyllaceae			S	S	
<i>Carex piluifera</i>	Cyperaceae	S				
<i>Erica arborea</i>	Ericaceae			S	S	S
<i>Rosmarinus officinalis</i>	Ericaceae					D
<i>Medicago lupulina</i>	Fabaceae				S	
<i>Trifolium</i> sp.	Fabaceae				S	
<i>Lavandula angustifolia</i>	Lamiaceae	S	S			
<i>Teucrium scorodonia</i>	Lamiaceae	S				
<i>Picea abies</i>	Pinaceae	S				
<i>Pinus mugo rotundata</i>	Pinaceae	D				
<i>Pinus mugo uncinata</i>	Pinaceae		D			
<i>Pinus nigra</i>	Pinaceae			D	S	
<i>Pinus sylvestris</i>	Pinaceae	S	S			
<i>Anthoxanthum odoratum</i>	Poaceae	S				
<i>Anthoxanthum</i> sp.	Poaceae			S	S	
<i>Briza</i> sp.	Poaceae			S	S	S
<i>Poa annua</i>	Poaceae	S	S		S	
<i>Poa pratensis</i>	Poaceae	S				
<i>Poa</i> sp.	Poaceae			S	S	S
<i>Polygonum aviculare</i>	Polygonaceae				S	
<i>Rumex acetosa</i>	Polygonaceae	D				
<i>Rumex acetosella</i>	Polygonaceae	S				
<i>Rumex bucephalophorus</i>	Polygonaceae				S	
<i>Alchemilla glaucescens</i>	Rosaceae	S	S			
<i>Potentilla erecta</i>	Rosaceae	S				
<i>Sorbus aucuparia</i>	Rosaceae	S				
Herbs not determined	Several families		S	S	S	S
Grasses not determined	Poaceae			S	S	S
Insects not determined	Parahyponomeutidae			S		
Insects not determined	Aphidina	S				
Insects not determined	Psyllina	S				

D dominant food source, *S* subordinate food source

sites of mainland citril finches (Dorka 1986; Borrás and Senar 1991; Kilzer and Blum 1991; Glutz von Blotzheim and Bauer 1997; Hölzinger and Dorka 1997; Förschler 2001a, 2001b; Borrás et al. 2003; Förschler et al. 2005). The only exception known so far are citril finches breeding in alder *Alnus virididis* thickets (Mingozzi and Bocca 1986). The seeds of the alder probably accomplish the same function as the seeds of conifers.

The extensive use of pine seeds as a staple diet (Förschler 2001a; Borrás et al. 2003) may be linked to their high nutritional content and their seed production phenology (Pulliainen 1974). Valera et al. (2005) showed that serins have specialised to a single plant species *Diploaxis virgata*, which comprises the majority of the diet of both adults and offspring due to its high protein

and energy content. Similarly, pine seeds contain a much higher portion of protein and fat than do spruce seeds (Pulliainen 1974). If both pine and spruce seeds are available, citril finches show strong preferences for pine seeds (V. Dorka, personal communication, and personal observations). Consequently, it is highly likely that spruce seeds are of interest only in years of mass seed reproduction (Kilzer and Blum 1991; Förschler 2001a). Furthermore, it seems that seed production of spruces is too irregular to form a reliable basic food source for a bird with high breeding site fidelity such as the citril finch. In contrast, mountain pines are known to produce yearly seeds without larger fluctuations (Hölzinger and Dorka 1997; V. Dorka in Glutz von Blotzheim and Bauer 1997; Förschler 2001a).

In addition to conifer seeds, abundant herbs and grasses are also of importance in the nutrition of mainland citril finches during the breeding period. Among these plants, dandelion plays a central role in the Black Forest (Hölzinger and Dorka 1997; Glutz von Blotzheim and Bauer 1997; Förschler 2001a; this study), in the Pyrenees (Borras et al. 2003; Förschler et al. 2005; this study) and in the Alps (Maestri et al. 1989; Glutz von Blotzheim and Bauer 1997).

Corsican (citril) finches are generally expected to have broader feeding niches than mainland citril finches as they breed in various habitats from sea level up to high elevations (Thibault 1983; Blondel et al. 1988; Thibault and Bonaccorsi 1999). In our study, we also found Corsican finches breeding on Corsica from almost sea level to mountain zones up to 2,000 m high, but the highest abundance occurred similar to the mainland citril finches in the pine dominated semi-open mountains from 900 m to 1,500 m a.s.l. (personal observations).

In contrast to the pine-seed dependence of the mainland citril finches, we found insular Corsican finches from Corsica consumed a great variety of herb seeds during the breeding period, especially the small seeds of the annual shepherd's purse, which was extremely abundant at all breeding localities. The seeds of suitable pine species, especially of the Corsican subspecies of black pine *Pinus nigra laricio*, did not play a large role for the finches in the study year. It is not clear whether this was caused by an insufficient seed availability or whether it can be regarded as a general behavioural trend in Corsican finches. The seeds of other abundant pine species in Corsica, such as maritime pines *Pinus pinaster*, aleppo pines *Pinus halepensis* and stone pines *Pinus pinea*, are not suitable for the species, because their seeds are clearly too large and hard.

The Corsican finches on the nearly pine-free island of Capraia are living under particular habitat conditions due to the small size and the much lower elevations of the island (Moltoni 1975; Lambertini 2000, 2002). We observed most finches on Capraia to forage on various herbs. Especially rosemary played a predominant role and was often consumed in groups with other finches such as serins, linnets *Carduelis cannabina* and greenfinches *Carduelis chloris*.

So far, our observations from Corsica and Capraia indicate that insular Corsican finches differ considerably from mainland citril finches in their diet selection during the breeding season, with a clearly higher portion of herb seeds instead of pine seeds in their nutrition. However, our observations on diet composition of Corsican finches in Sardinia revealed that this is not necessarily the case for all sub-populations. Here, Corsican finches showed a foraging behaviour very similar to that of mainland citril finches. Black pine

seeds provided nearly half of the food during the breeding season and seeds of herbs and grass were of only minor importance. Furthermore, Sardinian birds showed a considerably high preference for larvae and pupae of ermine moths (Parahyponomeutidae), living in large numbers on tree heath during May and June. A similar behaviour was also found in mainland citril finches in the Black Forest which temporarily used aphids as an additional food source. This indicates that both citril and Corsican finches may, under specific conditions (e.g. abundant occurrence of insectivorous food), show a diet shift to insectivorous nutrition as found in other seed-eating birds. In contrast, in serins, neither adults nor nestlings fed on insects during breeding season (Valera et al. 2005).

To conclude, we were not able to confirm clear differences in food choice between mainland citril and insular Corsican finches due to the different habitat selection, as implicated by the hypothesis of increased niche breadth, shift in feeding behaviour (Blondel 1985; Blondel et al. 1988) and the evolutionary history of the Corsican finch (Sangster 2000; Sangster et al. 2002). In contrast, food choice behaviour of both forms was highly adaptive and mostly reflected the availability and fruiting times of adequate food resources in the different localities (personal observations). Abundant seeds of optimal size were favoured as basic food plants during breeding season. Such a behaviour indicates that citril and Corsican finches perform active food selection as described by Glück (1980b), who demonstrated that goldfinches show clear preferences for specific food plants. This selective behaviour of the finches can be explained by differences in the energy content of the seeds, productiveness and abundance of certain plants, and the time and effort it takes for the finches to get to the food plant and to handle the seeds. As documented for serins during breeding season (Valera et al. 2005), the nutritional benefit of plants due to their high protein and energy content plays a dominant role for the food selection. It is highly likely that, in citril and Corsican finches, plants with low feeding efficiency are only of interest outside the breeding season as observed in goldfinches (Glück 1980a, 1986). In line with this observation, in all studied populations the carbohydrate-rich seeds of grasses played only a minor role during the breeding period, because they do not contribute enough protein to the specific physiological demands for breeding (Sabel 1965). This contrasts with the view that citril finches generally prefer grass seeds (Märki 1976; Cramp and Perrins 1994). Nonetheless, a great variety of grass seeds gain importance after breeding (Sabel 1965; Mau 1980; Förschler 2001a; Borras et al. 2003), probably because they become extremely abundant and the foraging efficiency for their small seeds might be much higher at that time of the year.

Zusammenfassung

Makrogeographische Variation in der Nahrungswahl von Festlandpopulationen des Zitronenzeisiges *Carduelis [citrinella] citrinella* und Inselpopulationen des Korsenzeisiges *Carduelis [citrinella] corsicanus*

Wir untersuchten die Nahrungswahl von Zitronenzeisigen *Carduelis [citrinella] citrinella* im Schwarzwald und den Katalonischen Vor-Pyrenäen im Vergleich zur Nahrungswahl des nah verwandten Korsenzeisiges *Carduelis [citrinella] corsicanus* auf Sardinien, Korsika und Capraia. Dabei interessierten wir uns insbesondere für die Hauptnahrungspflanzen während der Brutzeit. Während unserer Untersuchungen ernährten sich sowohl die Zitronenzeisige in den Katalonischen Vor-Pyrenäen als auch diejenigen im Schwarzwald überwiegend von Samen der Bergkiefer und von denen des Löwenzahns. Im Gegensatz dazu fraßen Korsenzeisige auf den Mittelmeerinseln Korsika und Capraia hauptsächlich die Samen verschiedener Kräuter während der Brutperiode. In Korsika spielten dabei im Untersuchungsjahr Hirtentäschelsamen eine herausragende Rolle während auf der kleinen Mittelmeerinsel Capraia Rosmarin von besonderer Bedeutung war. Unsere Beobachtungen am Korsenzeisig passen gut zu den aufgrund einer generellen Nischenerweiterung zu erwartenden Unterschieden in der Nahrungswahl im Vergleich zum Zitronenzeisig. Allerdings war im Gegensatz zu dieser Annahme die Nahrungswahl der Korsenzeisige auf Sardinien in unserer Studie sehr ähnlich derjenigen in den untersuchten Zitronenzeisig-Populationen. Hier fraßen Korsenzeisige insbesondere die Samen von gut fruchtenden Schwarzkiefer-Beständen während der Brutzeit. Es konnten also keine allgemeingültigen Unterschiede in der Nahrungswahl der Teil-Populationen des Zitronen- und Korsenzeisiges gefunden werden. Demzufolge kann die Nahrungswahl bei beiden Formen (wahrscheinlich Allospesies) als sehr adaptiv betrachtet werden und in verschiedenen Brutgebieten können sehr unterschiedliche Nahrungspflanzen besondere Bedeutung erlangen. Die Bevorzugung bestimmter Pflanzenarten während der Brutzeit hängt dabei wohl viel mehr von deren Häufigkeit, Zugänglichkeit und Energiegehalt ab.

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