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**REVIEW** 

# Information transfer about food as a reason for sociality in bats

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#### **ABSTRACT**

- Information transfer about food is a potential reason for sociality in many animals. If an animal is better informed, it should then be better able to adjust its behaviour and reduce the uncertainty of finding food in a variable world.
- 2. Given the remarkable range of social systems and ecological niches of bats throughout the world, bats are well-suited as a model to review mechanisms and fitness consequences of information transfer about food. The aim of this manuscript was to conduct a systematic literature review for mechanisms for information transfer and their potential fitness consequences for bats.
- 3. Information transfer behaviour is found in bats under various ecological conditions, including in groups of males in temperate regions, in groups of males or females in subtropical regions, and in mixed groups in tropical regions. Bats can learn about food indirectly, for example via chemical cues carried by the breath and body of frugivorous bats, or via acoustic cues from feeding buzzes from insectivorous bats. The majority of playback studies in captivity and in the wild showed stronger intra-specific and inter-specific attraction of bats to feeding buzzes than to silence controls or to search phase calls. Bats can also transfer information directly, via signals intended to attract, to repel or even to jam the echolocation of conspecifics.
- 4. Social foraging in bats can be categorised as local enhancement, information-centre hypothesis, group foraging or food sharing, depending on the type of information transfer and the food sources used. Fitness consequences of information transfer from the actor's and the recipient's perspective remain poorly investigated to date. Recent studies in insectivorous bats suggest a balance of benefits from prey searching and costs of acoustic interference that may condition group size.
- 5. The future use of a wide array of methods promises to reveal exciting insights about mechanisms and fitness consequences of information transfer by bats about food.

#### INTRODUCTION

For animals that choose to live in groups, the inclusive fitness (see Glossary for definition) benefits of group living should outweigh the costs (Hamilton 1964, Lehmann & Keller 2006). Costs of living in groups include, for example, an increased parasite burden, competition, and misdirected parental care (Brown & Brown 1986, Lewis et al. 2001, Krause & Ruxton 2002,

Yom-Tov 2008). The benefits of sociality include predator dilution effects (Foster & Treherne 1981), enhanced thermoregulation (Campbell et al. 2018), and many co-operative behaviours (e.g. allogrooming, joint efforts in the building of shelters; Ward & Zahavi 1973, Milinski 1987, Axelrod & Dion 1988, Crowley 1996, Dugatkin & Mesterton-Gibbons 1996, Beauchamp et al. 1997, Buckley 1997, Hatchwell & Komdeur 2000, Krause & Ruxton 2002).

Glossary

Bats are a promising system for the study of the causes and consequences of sociality, considering the more than 1300 known species that live in a broad range of social systems and ecological niches over different climates. Sound and olfaction appear as particularly important signalling modes for bats to communicate (Chaverri et al. 2018). Temperate bats often form groups seasonally, while tropical bats tend to gather year-round (McCracken & Wilkinson 2000). With the exception of a few species that make tents or roosts, bats cannot build roosts, but are highly dependent on day roosts that protect them from weather and predators. Roost limitation appears therefore as one potential cause for bat sociality, for example if bats rely on caves and tree cavities (Kerth 2008). Social thermoregulation (mutual warming) appears as an important reason for sociality in temperate bats. In spring and summer, adult females with their juveniles form clusters, which allows females to save energy by reducing heat loss, and offspring to accelerate their growth and improve survival (Humphrey 1975, McCracken & Wilkinson 2000, Zubaid et al. 2006). During hibernation, bats benefit from clustering by minimising heat loss and associated energy expenditure (Boyles et al. 2008).

In addition to roost limitation and the benefits of social thermoregulation, information transfer about food, especially ephemeral patches such as insects or fruits, represents another reason for sociality in bats. If an animal is better informed, it should be better able to adjust its behaviour and, for example, reduce the uncertainty of finding food in a variable world (Dall et al. 2005). Information transfer about food is known to occur in groups of male bats in temperate regions (Safi & Kerth 2007), in groups of males or females in subtropical regions (Levin et al. 2013, Cvikel et al. 2015), and in mixed groups in tropical regions (Dechmann et al. 2009, 2010). Information transfer about ephemeral food patches can indeed increase foraging efficiency (Safi & Kerth 2007, Dechmann et al. 2009, 2010). By observing the behaviour of others, animals can learn about the location, quantity, and quality of food (Horn 1968, Krebs 1974), which can increase feeding efficiency, reduce predation risk, and reduce competition. Information transfer about food patches has already been shown to occur in both sub-orders of the order Chiroptera, including in the family Rhinopomatidae in the suborder Yinpterochiroptera (Cvikel et al. 2015) and in the families Molossidae, Noctilionidae, Phyllostomidae and Vespertilionidae in the suborder Yangochiroptera (Page & Ryan 2006, Safi & Kerth 2007, Dechmann et al. 2009). A phylogenetic analysis of two bat families (Molossidae and Vespertilionidae) by Safi and Kerth (2007) suggests repeated convergent evolution of information transfer in bats. The aim in this manuscript was to review the diversity of mechanisms for information transfer in bats and their potential fitness consequences in relation to sociality.

Altruism:	A behaviour which is costly to the actor and beneficial to the recipient; cost and benefit are defined based on the lifetime direct fitness consequences (West et al. 2007).
Bat passes:	Bat passes have different definitions depending on the study. A bat pass can for example be defined based on a given radius around the speaker (Balcombe & Fenton 1988) or based on echolocation recordings (Hügel et al. 2017).
Direct fitness:	Component of inclusive fitness gained from impacts on offspring production (West et al. 2007).
Feeding buzz:	The feeding buzz is characterized by a series of short pulses at a high repetition rate (up to 180-200 kHz), usually in one but sometimes in two or more groups (Schnitzler & Kalko 2001).
Inadvertent social information:	A class of cues that are produced inadvertently by individuals engaged in some activity, such as foraging, fighting, or mating (Danchin et al. 2004)
Inclusive fitness:	The sum of direct and indirect fitness benefits (West et al. 2007).
Indirect fitness:	Component of inclusive fitness gained from aiding relatives (West et al. 2007).
Information- center (hypothesis):	Individuals at the roost obtain information on the location of food (Ward & Zahavi 1973).
Local enhancement: Mutual benefit:	The presence of foragers at a patch increases its conspicuousness to others (Buckley 1997).  A behaviour benefitting both actor and recipient

Signals: Sources of socially acquired information that function to influence the behaviour of others.

(West et al. 2007)

(Griffin et al. 1960)

They are generally studied as communication (Dall

The search phase is fairly straight flight in which

the pulse repetition rate is relatively low, although

the bat is evidently ready to attack flying insects

et al. 2005).

Social calls: Acoustic communication signals in bats. Social cues: A type of inadvertent social information that

> conveys discrete information about the presence or absence of some feature (e.g. presence or absence of predators or the spatial location of a

food patch; Dall et al. 2005).

## **METHODS**

Search phase

calls:

Three complementary sources of information were used to search for relevant articles: 1) a private library built over several years, 2) direct topic searches on Google scholar, and 3) the reference sections of the selected Y. Gager Food and sociality in bats

Table 1. Social foraging classes in bats.

Level of cooperation	Social foraging class	Definition	Information transfer	Food sources	Suggested in the following species	
Non-cooperative foraging	Solitary	Solo hunting	No response to other individuals	All types of single prey items and patches	Important for all bats	
3 3	Group	Independent convergence on highly vulnerable prey, success not enhanced, prey not shared	No response to other individuals	All types of patches	Possible for many species	
Cooperative foraging	Local enhancement	Bats cue on conspecifics and heterospecifics foraging on similar diet	Acoustic cues (e.g. feeding buzzes)	Patches with spatial unpredictability	Possible for many species	
	Information center hypothesis	Bats learn of food source from behaviour of roost-mates at roosts	Chemical cues (e.g. carried on the breath, bodies or urine of conspecifics)	Patches with spatial predictability and temporal ephemerality of several hours/weeks (e.g. insects, flowers or fruits)	Carollia perspicillata, Nycticeus humeralis, Uroderma bilobatum (Wilkinson 1992, Ratcliffe & Ter Hofstede 2005, O'Mara et al. 2014)	
	Group foraging	Bats flock to search for resources	Acoustic cues (e.g. feeding buzzes), acoustic signals (e.g. social calls)	Patches with spatial unpredictability and temporal ephemerality (e.g. insects, flowers or fruits)	Molossus molossus, Noctilio albiventris, Phyllostomus hastatus (Wilkinson & Boughman 1998, Dechmann et al. 2009, 2010)	
	Food sharing	Bats share food directly with known conspecifics	Acoustic signals (e.g. social calls)	Shareable and transportable food (e.g. blood regurgitates, insects)	Desmodus rotundus, Micronycteris microtis (Carter & Wilkinson 2013, Geipel et al. 2013)	

articles. The categories and definitions of social foraging classes were adapted from the work of Ellis et al. (1993) on raptors. To document the effect on bats of playback of feeding buzzes, I compared how the studied parameter (e.g. activity ratio or responses) differed between playback of feeding buzzes and silence or search call playbacks.

# **RESULTS AND DISCUSSION**

## Social foraging classes

I categorised social foraging classes of bats based on various parameters, including the level of cooperation and the type of information transfer and food sources (Table 1). The first level of cooperation – non-cooperative foraging – is divided into solitary and group foraging, and implies no response to other individuals. The second level of cooperation – cooperative foraging – implies information transfer between individuals and is divided into four classes: 1) local enhancement, 2) information centre hypothesis, 3) group foraging, and 4) food sharing.

First, local enhancement relies on aggregation of predators at a food patch as a social cue for prey availability, typically seabirds foraging on pelagic fish. A parallel example in bats is conspecifics and heterospecifics with similar diet foraging on spatially unpredictable insect patches and using feeding buzzes as an acoustic cue for prey availability. Second, the information centre hypothesis (Ward & Zahavi 1973) requires information transfer between knowledgeable and naive individuals at the roost and subsequent following to the foraging grounds. Such behaviour is only possible in the case of food patches with spatial predictability and temporal ephemerality (several hours to weeks), for example 1.65  $\pm$  0.2 days (n = 24) for insect patches,  $4.12 \pm 0.92$  days (n = 25) for flower patches on Ochroma lagopus and 6.29 ± 0.82 days for fruit patches on Cecropia trees (Wilkinson & Boughman 1999). Naive individuals can collect public information from roost-mates via chemical cues on breath, body (Ratcliffe & Ter Hofstede 2005, O'Mara et al. 2014) and maybe urine (Wilkinson 1992). Third, group foraging consists of individuals flocking to search for food patches with spatial unpredictability and temporal ephemerality, typically patches of insects. Bats specialised on insect patches possess narrow wings adapted

**Table 2.** Comparison of studies in which responses of bats to playbacks of feeding buzzes were recorded. FB, feeding buzz; FB BWD, feeding buzz played backwards. The column 'Effect' contains information about how the studied parameter (e.g. activity ratio or responses) reacts when exposed to two different types of calls (columns 'Call' vs. 'Comparison'). The effect can be either a decrease '-', no change '0' or an increase '+' of the studied parameter. For example, there is a negative response '-' of *Euderma maculatum* when playing feeding buzz backwards in comparison to silent control or feeding buzz.

Species	Family	Call	Comparison	Parameter	Effect	Reference
Euderma maculatum	Vespertilionidae	FB BWD	FB/Silent control	Responses	_	Leonard and Fenton (1984)
Saccopteryx bilineata	Emballonuridae	FB	Search calls	Activity ratio	0	Übernickel et al. (2012)
Tadarida brasiliensis	Molossidae	FB	Search calls/Silent control	Number of bat calls in 10 min	+	Gillam (2007)
Noctilio albiventris	Noctilionidae	FB	Pre-playback silence	Average number of counts (approach)	+	Dechmann et al. (2009)
Noctilio albiventris	Noctilionidae	FB	Search calls	Activity ratio	+	Übernickel et al. (2012)
Noctilio leporinus	Noctilionidae	FB	Search calls	Activity ratio	+	Übernickel et al. (2012)
Rhinopoma microphyllum	Rhinopomatidae	FB	Search calls	Approaches	+	Cvikel et al. (2015)
Euderma maculatum	Vespertilionidae	FB	Silent control/FB BWD/ Artificial call	Responses	+	Leonard and Fenton (1984)
Myotis lucifugus	Vespertilionidae	FB	Silent control/FB BWD	% of response	+	Barclay (1982)
Lasiurus borealis	Vespertilionidae	FB	Silent control	Mean bat passes per trial	+	Balcombe and Fenton (1988)
Nyctalus noctula	Vespertilionidae	FB	Search calls	% of bat passes	+	Dorado-Correa et al. (2013)
Myotis capaccinii	Vespertilionidae	FB	Search calls	% of bat passes	+	Dorado-Correa et al. (2013)
Pipistrellus nathusii	Vespertilionidae	FB	Search calls	% of bat passes	+	Dorado-Correa et al. (2013)
Myotis daubentonii	Vespertilionidae	FB	Search calls	% of bat passes	+	Dorado-Correa et al. (2013)
Myotis capaccinii	Vespertilionidae	FB	Pre/post-playback silence	Proportion of total flight time spent in playback compartment	+	Hügel et al. (2017)
Myotis capaccinii	Vespertilionidae	FB	Pre/post-playback silence	Number of bats passes/ min ( <i>Myotis daubentonii</i> & <i>Myotis capaccinii</i> )	+	Hügel et al. (2017)
Myotis daubentonii	Vespertilionidae	FB	Pre/post-playback silence	Number of bats passes/ min ( <i>Myotis daubentonii</i> & <i>Myotis capaccinii</i> )	+	Hügel et al. (2017)

to open-air foraging (Safi & Kerth 2007), and rely on acoustic cues such as feeding buzzes (e.g. Dechmann et al. 2010) or acoustic signals such as screech calls (Wilkinson & Boughman 1998). Despite short-term patch duration, the frequent occurrence of such patches can guarantee a significant food source throughout a period; for example, nuptial flights of ants (Camponotus sp.) form up to 90% of the diet of Rhinopoma microphyllum during the summer (Levin et al. 2009). Finally, food sharing involves signalling between individuals and direct exchange of shareable and transportable resources, such as blood regurgitates in Desmodus rotundus (Carter & Wilkinson 2013) and insects provided during post-weaning in Micronycteris microtis (Geipel et al. 2013).

#### Indirect transmission of information

The provision of inadvertent social information typically means that individuals unavoidably produce different types of social cue (e.g. acoustic and chemical) that can be

utilised by recipients in the vicinity. Echolocation calls emitted by ca. 90% of all bat species constitute important cues for conspecifics (Fenton 2003, Gillam 2007, Dechmann et al. 2009). Immediately before attempting to capture prey, some bats emit a series of short pulses at a high repetition rate known as a feeding buzz (Schnitzler & Kalko 2001). By eavesdropping, individuals can therefore learn about the abundance of insects from a large distance. For example, the distances at which feeding buzzes are audible to bats have been estimated to be 35-40, 54 and 160 m, respectively in Noctilio albiventris, Molossus molossus, and Rhinopoma microphyllum (Dechmann et al. 2009, 2010, Cvikel et al. 2015). Global positioning system (GPS) loggers with acoustic microphones showed that individuals of the insectivorous bat Rhinopoma microphyllum spend a substantial part of their foraging periods (41%  $\pm$  14%; mean ± standard deviation percentage) less than 150 m from conspecifics, in order to improve prey detection (Cvikel et al. 2015). Several experimental studies in captivity and in the wild have shown the strong attraction Y. Gager Food and sociality in bats

of different bat species to playbacks of intraspecific feeding buzzes (Table 2).

Behavioural reactions of bats to feeding buzzes are experimentally assessed by comparing a certain parameter (e.g. number of response calls or bat passes) when playing either a feeding buzz or a control sound (e.g. silence, search phase calls; Table 2). Playback protocols should ideally include all three treatments (feeding buzz, other sounds such as search phase calls, and silence) to evaluate whether bats are attracted to any sound, or to the feeding buzzes in particular. Positive reactions to feeding buzzes were observed in the wild for 11 bat species, mostly Vespertilionidae, but also one Molossidae (Gillam 2007), two Noctilionidae (Dechmann et al. 2009, Übernickel et al. 2012) and one Rhinopomatidae (Cvikel et al. 2015). Positive reactions were also demonstrated in captivity for Myotis capaccinii (Hügel et al. 2017). An absence of response was observed in Saccopteryx bilineata exposed to both search phase calls and feeding buzzes. The only negative reaction was observed for a non-natural situation, when Euderma maculatum flew away from the speaker when exposed to a feeding buzz broadcasted backwards (Leonard & Fenton 1984). Additionally, at least three studies have already shown positive reactions to the playback of interspecific feeding buzzes in Noctilionidae Vespertilionidae (Übernickel et al. 2012, Dorado-Correa et al. 2013, Hügel et al. 2017; Table 2).

Frugivorous bats can evaluate chemical cues carried on the breath and bodies of conspecifics, both in captivity and in the wild, to learn about familiar and novel food sources (Ratcliffe & Ter Hofstede 2005, O'Mara et al. 2014, Ramakers et al. 2016). The smell of fresh urine of individuals of Nycticeus humeralis that had successfully foraged has also been suggested as a chemical cue used by unsuccessful foragers to choose to follow a successful forager during its next foraging bout (Wilkinson 1992). Information transfer appears here as an important mechanism to learn about familiar food sources that may be of low quality or ephemeral, as well as novel sources that can be unknown and potentially toxic. An experiment in captivity showed that the frugivorous Uroderma bilobatum ate more food demonstrated to it by non-roostmates than by roost-mates, providing support for the novel social partner hypothesis (Ramakers et al. 2016). Information about familiar food sources can therefore be used to reduce the costs associated with home-range monitoring, whereas information about novel food sources can be used to find sources of food (Ratcliffe & Ter Hofstede 2005). Both mechanisms potentially allow bats to pool collective information and survive resource bottlenecks (O'Mara et al. 2014, Ramakers et al. 2016). Social groups of bats may therefore function as information centres, as described in birds (Ward & Zahavi 1973), suggesting that inexperienced individuals follow

knowledgeable individuals from the roost to foraging sites. Information transfer between group members has been clearly demonstrated in frugivorous bats (e.g. Ratcliffe & Ter Hofstede 2005, O'Mara et al. 2014), and has been suggested in an insectivorous species (Wilkinson 1992). A few radio-tracking studies suggest that bats of the same roosting group travel together (e.g. Wilkinson 1992). One publication reports that roost-mates were netted at the same foraging site (Wilkinson & Boughman 1998), but firm evidence that bats follow knowledgeable individuals from the colony to food patches in the wild is still lacking.

#### Direct transmission of information

Very little is known about signals used by bats to communicate about food. At least three types of so-called social call can be associated with food searching or exploitation: contact calls, used to recruit and coordinate; territorial calls, used to defend food patches, and jamming calls, used to cause other bats to miss insect targets. Wilkinson and Boughman (1998) suggested that Phyllostomus hastatus uses screech calls as contact calls to recruit and coordinate foraging. Other studies suggest that territorial calls are used to fend off other bats of the same species when food is scarce, following the food-patch defence hypothesis. The frequency of these agonistic calls increases with the number of bats in the foraging area, and also with declining insect availability (Belwood & Fullard 1984, Racey & Swift 1985, Barlow & Jones 1997). Experimental playback of social calls produced by foraging Pipistrellus pipistrellus and Pipstrellus pygmaeus showed a significant reduction of bat activity in comparison to control trials (Barlow & Jones 1997). Such food-patch defence (of trees with nectar, flowers and fruits, using screech calls) was also hypothesised in Phyllostomus hastatus (Wilkinson & Boughman 1998). Additionally, a peculiar type of jamming call with sinusoidal frequency-modulated ultrasonic signals (sinFM calls) that interfered with the echolocation of conspecifics attacking prey has been recently shown in Tadarida brasiliensis (Corcoran & Conner 2014). Bats were 86% and 77% less likely to capture insects in the presence of conspecific-produced sinFM calls than without these calls, at two different field sites. Experimental playback of sinFM calls to individual bats attacking moths also decreased capture success by 74% in comparison to no playback. Another study was focused on *Eptesicus fuscus*, a species whose echolocation calls overlap with the sin FM calls of Tadarida brasiliensis. The playback of sinFM calls from Tadarida brasiliensis did not affect the capture rate of tethered moths by Eptesicus fuscus, although they did elicit echolocation changes (Jones et al. 2018). More research is required to determine if these sinFM calls are jamming or deterring other bats.

# Fitness consequences of information transfer

Both direct and indirect transmission of information can have positive or negative fitness consequences for the actor and the recipient of this information. Different categories of consequences can be described: mutual benefit (+/+), altruism (-/+), selfishness (+/-), and spite (-/-); West et al. 2007). Mutual benefits (+/+) from information transfer in bats could include coordinated and enhanced prey searching, as well as food patch defence. Fieldwork and comparative studies suggest that individuals in male aggregations of temperate species and mixed-sex groups in some tropical species benefit from information transfer in groups through enhanced prey searching (e.g. local enhancement) and potentially also through more effective tracking of the dynamic resource (Safi & Kerth 2007, Dechmann et al. 2009, 2010). Mutual benefits from food-patch defence are also suggested for roost-mates feeding on patches of insects and on trees with nectar, flowers and fruits (e.g. Barlow & Jones 1997, Wilkinson & Boughman 1998). Selfishness (+/-), benefitting only the actor, is likely to occur in the context of territorial calls of single individuals, as it does in Pipistrellus pipistrellus (Racey & Swift 1985). No evidence could be found for potential benefits of information transfer in terms of fitness, for example as a result of eavesdropping in echolocating bats. Such benefits remain difficult to quantify, especially in the long term. Recent work in echolocating bats suggests that there are trade-offs between the benefits of information transfer about ephemeral resources and the costs of acoustic interference (Cvikel et al. 2015, Gager et al. 2016). When searching for prey, an intermediate density of flying bats appears to be most efficient for foraging (Cvikel et al. 2015). This benefit-cost trade-off may lead to selection towards small social groups for bat species that are dependent on social information transfer about ephemeral resources (Gager et al. 2016).

#### **Future research**

Technological development offers new perspectives for research on information transfer about food in bats, including DNA metabarcoding, captivity experiments, acoustic playbacks and GPS combined with microphones. The classical method to elucidate bat diet, microscopic analysis of faecal material, relies on expert knowledge and reference collections of potential food items (insects, seeds, pollen, fruit fibres and leaf fragments). DNA metabarcoding is a recent development that allows the simultaneous sequencing of short genetic fragments from faeces, in order to identify bat dietary items such as arthropods and parts of plants. Metabarcoding is emerging as a great method to document diet richness and variability among species, populations, and individuals (e.g. Galan et al. 2017), with the potential to document the

ephemerality of food, for example. If bats are relying on patchy food sources, then metabarcoding of bat faeces should give insights about the use of food patches, including simultaneous consumption by group members and seasonality. Experiments in captivity as well as well as in the wild are great opportunities to learn about mechanisms of social learning, for example (Ratcliffe & Ter Hofstede 2005, Page & Ryan 2006, O'Mara et al. 2014). If bats can learn food association transfer through odour transfer from others, then naive bats exposed to a new odour of food eaten by a group member should be more likely to eat the same food. If bats are exposed to information of differing quality about two types of food, then they should favour the food associated with the most reliable information. The use of playbacks in captivity and in the wild also have great potential, for example for investigating the functions of the vast repertoire of social calls (e.g. Barlow & Jones 1997), or the reaction of different species to feeding buzzes (see the references listed in Table 2). If a type of social call (the contact call) has the function to attract bats, then playback of these social calls should increase the presence of conspecifics in the vicinity. If another type of social call (the territorial call) has the function to fend off other bats of the same species then playback of these social calls should decrease the presence of bats of the same species in the vicinity. If echolocating bats use information from feeding buzzes, then bats should be attracted to this stimulus in preference to white noise or another sound (e.g. search phase calls). Furthermore, miniature GPS devices, which can now potentially be combined with ultrasonic microphones, offer new perspectives for revealing bats' dynamic reactions to prey or conspecifics (Cvikel et al. 2015). If echolocating bats are eavesdropping on feeding buzzes to locate prey, then bats should aggregate more when a bat emits feeding buzzes. If social groups of bats function as information centres, then inexperienced individuals should follow knowledgeable individuals from the roost to foraging sites. If social foraging in echolocating bats improves prey searching success, then an artificial reduction in group size should result in increased foraging times or decreased body mass gain or foraging efficiency for similar foraging times. Further investigation of fitness-related parameters, such as foraging efficiency and survival, in relation to parameters such as group size, constitute other promising avenues of research. The diversity of bats, in terms of sociality as well as in terms of feeding strategies and sensory ecology, are a promise for new discoveries on the mechanisms and fitness consequences of information transfer in relation to food.

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