BEHAVIORAL RESPONSES TO A NOVEL FEEDING PROBLEM IN THE OLROG'S GULL LARUS ATLANTICUS

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ABSTRACT

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Behavioral innovation is considered an expression of behavioral flexibility and is a source of phenotypic plasticity in animals. In this study, we explored the main components of behavioral innovation (neophobia and exploratory behavior) with respect to social context and age in the Olrog's Gull *Larus atlanticus*. Twenty consecutive experimental sessions were performed, involving presentation of a plexiglass box containing food; the box could be opened and reached by pushing or pulling different lids, each leading to a food reward. Gulls were able to decrease their neophobic response throughout the course of the experiments. Fifty-three percent of individuals who entered the feeding station contacted the box. However, no successful box opening was recorded during this study. Age and social context did not affect latency to enter the feeding station or the time that the individuals invested in exploring the novel object. Social context affected contact flexibility (variation in the location on the box where the individual made contact); greater flexibility was recorded as the number of juveniles at the feed station increased and the total abundance of individuals decreased. Our study demonstrates how knowledge of the propensity to innovate can inform our understanding of the foraging behavior of Olrog's Gulls, with important implications to potential conservation concerns for this threatened species.

Key words: behavioral flexibility, conservation, Larus atlanticus, novelty response, Olrog's Gull

INTRODUCTION

Most animals have been exposed to environmental perturbations during their evolutionary history, but the increased speed of human-induced changes poses a challenge for many species. Urbanization, deforestation, and habitat fragmentation are examples of anthropogenic effects to which animals must adapt within a very short timescale (Sih et al. 2011, Tuomainen & Candolin 2011). These environmental modifications generally alter the interactions between species, differentially affecting their survival and reproductive success and resulting in changes in their diversity and distribution ranges (Sih et al. 2011). In this scenario, organisms often face new environmental conditions for which they may have to perform alternative actions in order to adapt to these novel situations (Ricklefs 2004). Organisms that inhabit moderately changing and complex environments benefit from high levels of behavioral flexibility (Sol et al. 2005). These behavioral adjustments are usually expressed relatively quickly, often within a single generation, and they can be induced by a wide range of signals and environmental variables (Van Buskirk 2014).

Behavioral innovation, defined as the generation of new behaviors or the modification of existing behaviors to solve novel problems, is a process that introduces new behavioral patterns into the repertoire of a species or population (Reader & Laland 2003). This process is considered an expression of behavioral flexibility in animals and is a rich source of phenotypic plasticity (Sol *et al.* 2005). The innovation process has important evolutionary implications because it influences the successful colonization of new habitats, the capacity to use novel resources, and the way in which organisms respond to changes in their environment (Reader & Laland 2003). Animals can vary in their propensity to innovate, even within the same species (Sol *et al.* 2012, Griffin & Guez 2014).

There are several factors that determine the occurrence and establishment of novel behaviors in a population. Key components of behavioral innovation include the novelty response, exploratory tendency, individual learning, and the ability to socially transmit learned behaviors (Reader & Laland 2003, Griffin & Guez 2014). Responses to novel stimuli, termed noetic styles (i.e., neophobia or neophilia, which are aversion or attraction responses, respectively; O'Hara et al. 2017), as well as exploratory behavior, determine the probability that animals will perceive, inspect, and probe a new resource, leading to innovation (Griffin & Guez 2014). In the same way, individual learning is one of the mechanisms that contributes to the establishment of an innovation (Dukas 2013, Brown 2014). This is because, through learning, individuals can incorporate a particular innovation into their behavioral repertoire; without this cognitive mechanism, an innovation cannot be repeated (and improved) in the future (Reader & Laland 2003, Tebbich et al. 2016). Further, social learning also influences the likelihood that an innovative behavior will be transmitted to other individuals, allowing it to spread within a population and across successive generations (Reader & Laland 2003, Griffin & Guez 2014, Tebbich et al. 2016).

The ability to solve novel feeding problems is one of the main correlates of behavioral flexibility, providing an ecologically significant assay to estimate the capacity to innovate (Lefebvre & Sol 2008). The typical test consists of presenting animals with an extractive foraging task that must be solved to access food (see Griffin & Guez 2014). This methodology has been used to study many species of reptiles, birds, and mammals (see Biondi *et al.* 2010, Benson-Amram & Holekamp 2012, Griffin *et al.* 2014, Chow *et al.* 2016). Studies like these usually identify factors influencing the solving capacity of individuals during an extractive foraging task. These factors are persistence (which is positively correlated with the success or initial speed of solving), flexibility in these attempts, neophobia level, and the duration of exploration before contact with the novel stimulus occurs. The results of these studies suggest that the capacity to solve novel problems is not just a cognitive attribute, but instead represents a dynamic set of cognitive, behavioral, and/or emotional characteristics (Griffin & Guez 2014).

The innovative problem-solving paradigm, like most cognitive abilities, has been studied most often under controlled conditions (Wasserman & Zentall 2006, Shettleworth 2009, MacDonald & Ritvo 2016). This is largely because, in captive settings, the environmental (both ecological and social) and individuals' internal factors (e.g., hunger, energy reserves)-characteristics that could influence cognitive performance-can be controlled. Additionally, using captive animals, the sample size does not represent a limiting factor, as generally occurs in field experiments. There is evidence, however, that problem-solving tests performed under controlled conditions suffer from low external validity, in some cases leading to marked differences in innovative capacity between individuals tested in captivity vs. those tested in natural settings (e.g., Webster & Lefebvre 2001, Ramsey et al. 2007, Benson-Amram et al. 2013). Some of the factors influencing such differences are (1) the alternative feeding sources available in the wild that might reduce participation in the problem-solving tasks, and (2) the social context that can influence the way individuals perceive and react to a novel feeding situation (Liker & Bókony 2009, Overington et al. 2009, Griffin & Guez 2014). Hence, although there is an increasing interest in cognition in wild animals, only a few studies have been performed so far with free-ranging animals tested under natural situations (e.g., Webster & Lefebvre 2001, Benson-Amram et al. 2013, Cauchoix et al. 2016, Pritchard et al. 2016, Cauchoix et al. 2017).

Seabirds are long-lived, inhabiting environments characterized by a high temporal variability (e.g., food availability, weather conditions), as well as being highly anthropized, offering ideal systems in which behavioral studies can be conducted. Additionally, some seabirds are considered dietary and habitat generalists, attributes known to be linked to innovative propensity (Overington *et al.* 2011). Recently,

there have been a few attempts to capture some components of behavioral innovation in gulls (Obozova et al. 2012, García et al. 2019, Goumas et al. 2019, Holman et al. 2019); however, much remains to be studied. The Olrog's Gull Larus atlanticus is endemic to the Atlantic coast of southern South America and is listed as Near Threatened by the IUCN (BirdLife International 2016) and Vulnerable in Argentina (MAyDS & AA 2017). Although the species was formerly considered to be one of the few gulls that specialized to feed solely on crabs, more recent studies have indicated that Olrog's Gulls may have broadened their diet (at least during the non-breeding season) by association with commercial and recreational fisheries (Berón & Favero 2009), among other factors. Recent studies have assessed the species' neophobic level in response to a non-familiar object close to their food (García et al. 2019); however, other potential mechanisms of behavioral innovation have not yet been studied. Considering the recent expansion of the species' trophic spectrum and associated behaviors, as well as recently reported conservation issues such as incidental mortality, behavioral flexibility mediated by the propensity for feeding innovation is likely to be of great relevance (Berón & Favero 2009). With this in mind, this study aimed to explore the behavioral reaction of Olrog's Gulls to a novel feeding problem presented in a natural setting. In particular, we assessed the roles of neophobia, exploratory behavior, persistence, and behavioral flexibility during problem-solving attempts, taking into account the social context and age of the individuals engaged in this activity.

MATERIALS AND METHODS

Study area

Field experiments were conducted during austral winter in 2017 at Mar Chiquita coastal lagoon, Buenos Aires Province, Argentina (37°46'S, 57°27'W), a Provincial Reserve and UNESCO Man and the Biosphere Reserve. Olrog's Gulls breed in areas south of Buenos Aires Province and in Patagonia (Yorio *et al.* 2005) using Mar Chiquita Reserve and neighboring coastal areas (500 km to the north) as winter quarters from April to September. Although juvenile individuals occur throughout the year in the study area, subadults and adults show a peak in abundance between June and August and are very scarce or absent during austral spring and summer.

As part of an on-going, long-term study on the behavioral ecology of Olrog's Gulls in the study area, we have marked individuals with



Fig. 1. Feeding station where the experiments on Olrog's Gulls were carried out during (A) control situations or (B) in the presence of the novel object used for neophobia and problem-solving tests.

leg bands since 2013. However, banded individuals were observed infrequently during the experimental sessions, limiting our capacity to interpret our results within the larger context.

Experimental protocol

Twenty consecutive experimental sessions were performed during July 2017. The experiments were performed once a day within a feeding station that consisted of a 2-m-diameter circle with food placed at the center (this circle was marked on the intertidal zone before starting the trials; Fig. 1). The station was established over the course of 20 d in the same area used by Olrog's Gulls as a foraging patch. All sessions were carried out early in the morning using shrimp and small pieces of bread as food. The experimental sessions were grouped in two blocks, which were defined during the fieldwork: (1) Block A consisted of 11 experimental sessions (days 1–11, neophobia test), and (2) Block B consisted of nine experimental sessions (days 12–20, problem-solving test).

Observations were conducted using binoculars (8×) and recorded with video camcorders for subsequent analysis in the laboratory. The video camera was positioned 5 m away from the feeding station, whereas the observer was 25 m away to minimize interference. Before starting each trial, the number of Olrog's Gulls in the vicinity of the feeding station (within roughly 40 m) was recorded by age-class. Three age classes were determined on the basis of plumage features (Harrison 1983): juveniles (1 year old), subadults (2–3 years old), and adults (\geq 4 years old, and potential breeders).

Neophobia test

Once gull visits were recorded at the feeding station, food was placed in the center of the station. During each trial, we offered 150 g of food. During this phase of the study, experiments were performed in daily sessions with three consecutive trials: (a) initiation, (b) control (i.e., familiar situation), and (c) treatment (i.e., novel situation). During the initiation, trial food was offered in the center of the feeding station. Thirty seconds after the first individual entered and consumed the first piece of food, the researcher interrupted the feeding, approached the station, and added food to keep the amount constant during the trial. Once the researcher returned to the observation point, birds approached again and consumed the food in the station; this second stage was



Fig. 2. Abundance of Olrog's Gulls attending the feeding station (white bars: adults, grey bars: subadults, black bars: juveniles) during the experimental days. Tests were conducted between 12.07.17 (day 1) and 31.07.17 (day 20).

considered a familiar situation and was classified as a control trial. Thirty seconds after the first individual entered and consumed food during the control trial, the researcher interrupted the feeding and placed a transparent plexiglass box containing food (novel object; dimensions $18 \text{ cm} \times 20 \text{ cm} \times 40 \text{ cm}$) in the center of the station, and additional food was placed around the box. This was considered a novel situation trial (i.e., treatment trial) and the duration of this trial was 780 sec. During this phase (Block A), the box was presented to gulls with all lids open so the food was accessible. Even though it is likely that individuals participating in the study varied, we assumed that the presentation of the "food" box at the feeding station on a daily basis would result in local birds habituating to the experimental conditions. We recorded the following variables: latency to enter, measured as the time taken for a bird to enter the feeding station and approach the box for the first time; latency to contact, measured as the time elapsed before a bird's first contact with the box; exploration time, measured as the time spent by individuals within the feeding station in the presence of the box; number of contacts, measured as the number of contacts made by a bird before it reached for the first portion of food; and latency to consume, measured as the time taken to consume food from the box for the first time. The level of neophobia was measured by the probability of entering (probability to enter) and the probability of consuming (probability to consume) food from the feeding station.

Problem-solving test

Once feeding from the opened box was recorded over three consecutive days, we started with the problem-solving tests (Block B). This test was designed following Webster & Lefebvre (2001) and Biondi et al. (2010) and consisted of the presentation of a closed plexiglass box containing food. The box could be opened and food reached by pushing or pulling different lids, each leading to different isolated pieces of food. The actions required of an individual to solve this problem are ecologically relevant because Olrog's Gulls are currently expanding their foraging habits, incorporating trophic items available in the environment that have been discarded from different recreational activities. The test also included daily sessions with three consecutive trials: initiation, control, and treatment, which were equivalent to those conducted during Block A. During the problem-solving test, we recorded the following variables: latency to enter; exploration time; number of contacts, measured as the number of attempts to open the box and reach for the first portion of food; total number of lids opened by each individual; and the *contact flexibility* expressed by individuals, estimated as the number of changes in contact sites of the box for those individuals that contacted the box more than once.

Statistical analysis

As part of the neophobia test (Block A), we analyzed the variability of different variables recorded each day. To do this, we performed Generalized Linear Models (hereafter GLMs) with a gamma error structure and Power -1 link function (Pinheiro & Bates 2000, Crawley 2007); the response variables tested were the latency to enter the feeding station, latency to contact the box, exploration time, and latency to consume from the open box. The number of contacts during the neophobia test was analyzed using GLMs with a Poisson error structure and log link function (Crawley 2007). To understand the neophobia of Olrog's Gulls, we also analyzed the probability to enter/consume in presence of a novel object in relation to session day, age class, total abundance of individuals, and abundance of juveniles close to the station. To this end, we used GLMs with a logit-linked binomial error structure (Pinheiro & Bates 2000, Crawley 2007). Two possible values were used for the response variable: zero if the individual did not enter/consume during the treatment trial; one if it entered/consumed.

As part of the problem-solving test (Block B), latency to enter the feeding station and exploration time were analyzed using GLMs with a gamma error structure and Power -1 link function; ageclass, total abundance of individuals, abundance of juveniles near the station, and session day were considered to be explanatory variables. The number of contacts and contact flexibility were analyzed using GLMs with a Poisson error structure and a log link function (Crawley 2007); the explanatory variables used were the same as those used in the previous analysis.

The variation in the distribution of abundances by age-class through the experimental sessions was analyzed using a chi-squared (X²) test (Zar 1999). All statistical analyses were carried out using R software version 3.4.2 (R Development Core Team 2017). All values are given as mean \pm standard error (SE) and all tests were two-tailed with a significance level of $\alpha = 0.05$.

Ethics statement

The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study were in accordance with the ethical standards of the institution or practice at which the studies were conducted and were approved by the Organismo Provincial para el Desarrollo Sostenible (OPDS, Disposition 066/16, Exp. N 2145-29322/12).

RESULTS

Two to 15 Olrog's Gulls were recorded at the feeding station; subadults were the most frequent age class attending the experiment ($X^2 = 51.01$, df = 2; P < 0.05; mean abundance juveniles: 1.40 ± 0.94; subadults: 4.80 ± 2.48; adults: 0.95 ± 1.15; n = 20; see Fig. 2). Gulls entered the feeding station during all control trials; however, under treatment trials, gulls entered the station in fewer than 80% of cases. Contact with the clear plexiglass box was registered in 50% of the treatment trials, largely during the problem-solving test (Block B).

Latency to enter during the control trials decreased throughout the experimental sessions; however, this trend was not significant (GLM, $\beta = -0.24$, t = -2.21, P = 0.06). During the treatment trials, latency to enter the feeding station decreased as the experimental sessions progressed (GLM, $\beta = -0.55$, t = -7.42, P < 0.05). There was no variation in the latency to contact the box or the number of contracts throughout the experimental sessions (GLM, contact latency: $\beta = -0.09$, t = -1.78, P = 0.11; number of contacts: $\beta = 0.37$, z = 1.46, P = 0.14). We observed an increase in the exploration time and a decrease in the latency to consume from the box in the experimental sessions (GLM, exploration time: $\beta = 0.42$, t = 3.68, P < 0.05; latency to consume: $\beta = -0.11, t = -2.47, P < 0.05$). The probability that gulls entered and consumed from the feeding station in the presence of the box increased as the experimental sessions progressed. Age, total abundance of individuals, and abundance of juveniles at the feeding station did not influence the probability to enter or probability to consume from the station (Table 1).

Forty-five percent of the recorded individuals within the experimental area entered the feeding station. The average time to approach the box was $117 \pm 163 \sec (n = 15)$. Fifty-three percent of individuals who entered the feeding station contacted the plexiglass box. The mean latency to first contact was $120 \pm 157 \sec (n = 8)$. No successful opening of the plexiglass box was recorded during the problem-solving test. There were no associations between the latency to enter and the exploration time with the tested factors (Table 2). A significant relationship was observed between the number of contacts with the box, the contact flexibility, and the social context; response variables increased as the abundance of individuals decreased and the abundance of juveniles increased within the feeding group (Table 2).

DISCUSSION

Our results indicate that Olrog's Gulls decreased their neophobic response to the plexiglass box throughout the course of the trials. Moreover, we found that an increase in the size of the feeding group negatively affected most of the variables related to performance of this task. On the other hand, we observed that the number of contacts with the box, as well as the flexibility observed in individuals during the opening attempts, was positively affected by the abundance of juveniles, which could be related to the inhibition of behavioral plasticity in the presence of dominant individuals (i.e., subadults) near the feeding station.

The percentage of individuals entering the feeding station and consuming the food offered in the feeding station during treatment trials was lower than in the control situation, indicating aversion to

TABLE 1
Models analyzing the response of Olrog's Gulls
to the neophobia test $(n = 81)$

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Response Variable ^a	Explicative Variable ^b	Category	Estimator (± SE)	z	Р
Prob_ent	Intercept		-5.49 ± 2.21	-2.47	0.01
	Age ^c	Juveniles	2.06 ± 1.28	1.61	0.10
		Subadults	1.75 ± 1.14	1.53	0.12
	Abun_TI		0.04 ± 0.16	0.27	0.78
	Abun_J		0.34 ± 0.49	0.69	0.48
	ED		0.32 ± 0.13	2.36	0.01
Prob_cons	Intercept		-7.03 ± 2.68	-2.61	<0.01
	Age ^c	Juveniles	2.14 ± 1.27	1.67	0.09
		Subadults	1.30 ± 1.13	1.15	0.24
	Abun_TI		0.22 ± 0.20	1.10	0.27
	Abun_J		0.19 ± 0.51	0.37	0.70
	ED		0.34 ± 0.16	2.07	0.03

^a Prob_ent = probability to enter; Prob_cons = probability to consume

^b Abun_TI = abundance of total individuals; Abun_J = abundance of juveniles; ED = experimental session day

^c Age of the observed individuals using adults as reference. Significant variables are shown in bold (P < 0.05).

the plexiglass box. This result was consistent with findings from a previous study addressing the neophobic behavior of this species facing novel objects (García et al. 2019). During treatment trials with the opened box, a decrease in the latency to enter the feeding station and consume food from the box was observed over time. Although the repeatability of the banded individuals attending to the trials was low (MVC unpubl. data), the probability that at least one individual was exposed a second time to the box could have led to the group to show decreased latencies compared to those initially registered, suggesting a habituation process towards the novel object. Previous field studies in birds have documented an attenuation of the fear response to risky or novel situations after repeated confrontations with such stimuli (e.g., Ensminger & Westneat 2012, Cavalli et al. 2018). However, without individual identification, there may be other possible explanations for our results, such as (1) the participation of less neophobic individuals as the experiment progressed, (2) the

TABLE 2Models analyzing the response of Olrog's Gulls
to the problem-solving test (n = 8)

increased participation of individuals that observed but did not enter

the feeding station as the experiment progressed, or (3) a combination

of both. The reduction of the aversive response to novel situations

Response Variable ^a	Explicative Variable ^b	Category	Estimator (± SE)	z	Р
LeT	Intercept		13.77 ± 4.26	3.23	0.04
	Age ^c	Subadults	-0.67 ± 0.81	-0.82	0.47
	Abun_TI		0.34 ± 0.40	0.87	0.44
	Abun_J		-1.03 ± 0.70	-1.48	0.23
	ED		-0.58 ± 0.30	-1.92	0.15
Exp_T	Intercept		9.15 ± 2.44	3.74	0.03
	Age ^c	Subadults	0.47 ± 0.46	1.01	0.38
	Abun_TI		-0.36 ± 0.22	-1.56	0.21
	Abun_J		0.14 ± 0.40	0.36	0.73
	ED		-0.26 ± 0.17	-1.53	0.22
Num_cont	Intercept		0.65 ± 2.55	0.25	0.79
	Age c	Subadults	-0.31 ± 0.37	-0.84	0.40
	Abun_TI		-0.58 ± 0.16	-3.48	<0.01
	Abun_J		0.84 ± 0.35	2.40	0.01
	ED		0.14 ± 0.17	0.83	0.40
Flex	Intercept		-5.67 ± 4.57	-1.24	0.21
	Age c	Subadults	1.09 ± 0.69	1.58	0.11
	Abun_TI		-1.03 ± 0.36	-2.82	<0.01
	Abun_J		2.06 ± 0.81	2.54	0.01
	ED		0.38 ± 0.28	1.35	0.17

^a LeT = latency to enter; Exp_t = exploration time; Num_ cont = number of contacts; Flex = flexibility expressed by individuals

- ^b Abun_TI = abundance of total individuals; Abun_J = abundance of juveniles; ED = experimental session day
- ^c Age of the observed individuals using juveniles as reference. Significant variables are shown in bold (P < 0.05).

through experience (i.e., learning) may have important implications to the way that gulls respond to changing conditions in their habitats. Future studies involving individuals that can be reliably identified could build on these initial findings.

As mentioned previously, group feeding allows individuals to obtain certain benefits related to reducing the risk of predation and the level of neophobia (e.g., Stöwe et al. 2006). Additionally, because large groups are likely to contain a diverse sample of individuals that differ intrinsically in their probability of success, their specific skills, their individual tendencies, or their past experience, group feeding might make individual birds more competent at solving the current problem (Burns & Dyer 2008, Liker & Bókony 2009). However, individuals feeding in groups may also incur costs related to increased competition and other social interactions (Krause & Ruxton 2002), and they may also exhibit increased neophobia and impaired social learning (i.e., the bystander effect, Overington et al. 2009). During our study, we observed that both the size and composition of the feeding group affects the performance of the individuals in the problem-solving test; the number of contacts and the flexibility expressed by the individuals increased in smaller feeding groups. These results are consistent with those reported by Overington et al. (2009), who observed that solitary birds were faster at solving a novel problem than those birds observed by conspecifics, suggesting that the feeding group slows innovation and reduces exploration time in novel situations. Conversely, our study shows that the abundance of juveniles within the feeding group positively affects the number of contacts and the flexibility expressed by individuals.

Reader & Laland (2003) proposed two hypotheses to explain why and how innovations occur in nature. The first hypothesis proposed that "necessity drives innovation" and suggested that individuals with poor competitive abilities are forced to develop novel strategies to survive, showing higher plasticity in their behaviors. The second hypothesis addressed differences in the capacity of individuals to solve innovative problems and proposed that the capacity to innovate is determined by cognitive skills, such as learning and reasoning. These hypotheses of necessity and capacity, however, are not mutually exclusive. In the present study, despite individuals approaching, exploring, and attempting to open the box-which are some of the key steps that lead to the occurrence of an innovation (Tebbich et al. 2016)-these individuals were not able to solve the task within the time limits and other trial conditions. Although we cannot exclude the possibility that this resulted from a lack of capacity, we also acknowledge that this study was undertaken in a natural context in which natural food sources were readily available, perhaps creating a lack of motivation and/or persistence during the task. Further studies should be performed under controlled experimental conditions and should include multiple tasks with different levels of difficulty to evaluate whether this failure in problem solving is associated with a lower cognitive capacity (e.g., Webster & Lefebvre 2001).

The modification of natural habitats in environments dominated by anthropogenic activities means that wildlife must adapt to these new conditions to survive. This ecological pressure may limit the ability of individuals to colonize and thrive in such environments (Chace & Walsh 2006). In some cases, the ability to develop new behaviors can be considered a predictor of long-term success of the species. Although we may assume that animals who survive within a changing environment have a high degree of behavioral flexibility, it is important to gain a clear understanding of the processes that underlie this flexibility so that we may understand how these processes could evolve. This knowledge may have implications for the protection of the species. In this study, evaluating neophobia, exploratory behavior, and the capacity to innovate in Olrog's Gulls allowed us to hypothesize about an individual's ability to adjust to anthropogenically modified environments. Future research in social learning within the species would benefit from using identifiable individuals in field tests, and from replicating studies in controlled experimental conditions. Studying behavioral flexibility and the role of social context in a rapidly changing human-influenced environment, especially for rare species with restricted diets, could be particularly relevant for the conservation of a locally threatened species.

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