Use of social information about novel food by juvenile solitary forktongue goby, *Chaenogobius annularis*

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Abstract

Animals use various forms of information to reduce uncertainty about the environment and make adaptive decisions. They can acquire information directly from the environment (personal information) or by observing other individuals' behaviour (social information). Since young animals in particular may benefit from acquiring social information owing to their lack of experience at this stage, social information in juveniles would be important even in solitary species. This possibility has, however,

been less studied in juvenile solitary fishes. We examined whether juveniles of the solitary forktongue goby, *Chaenogobius annularis*, use social information about novel artificial food (fish-food flakes) and a novel food location (water surface). We first tested whether feeding on the novel food is facilitated by past experience to confirm that *C. annularis* juveniles could learn this information: compared with naïve juveniles, juveniles that previously experienced the novel food showed significantly shorter latencies to begin feeding (at the surface or underwater, hereafter first feeding), and to feed on the water's surface (hereafter, surface feeding). We then compared feeding on novel food between naïve juveniles paired with an experienced juvenile and those paired with a naïve juvenile. Naïve juveniles paired with an experienced juvenile fed significantly more frequently and sooner in both first and surface feedings than the randomly chosen naïve juveniles in each naïve pair. These results suggest that *C. annularis* juveniles use social information to learn about food and that social information use by juveniles is widespread among vertebrates, regardless of their sociality.

Key words: adaptive decision, experience, demonstrator, fish, foraging, young individual

Introduction

Animals use various forms of information to reduce uncertainty about the environment and make adaptive decisions. They can acquire information directly from the environment (personal information) or by observing other individuals' behaviour (social information) (Danchin et al., 2004; Dall et al., 2005). Personal information can be obtained through trial-and-error tactics and direct access to physical habitat and resources; social information is based on signals or cues produced by other individuals engaged in activities such as breeding, mating, and foraging (Danchin et al., 2004). Social information indicates the quality and location of resources with which other individuals interact and reduces the time, energy, and predation risk associated with personal exploration of the environment (Danchin et al., 2004). However, since social information can become outdated or be inappropriate, it can be less reliable than personal information (Laland, 2004; Rieucau & Giraldeau, 2011). Animals should therefore use social information tactically, rather than indiscriminately, depending on their state and circumstances (Laland, 2004; Rendell et al., 2011; Kendal et al., 2018).

Young animals should benefit from using social information owing to their lack of experience and knowledge about the environment (Laland, 2004; Rendell et al., 2011; Kendal et al., 2018). Whether young use social information has been tested in various contexts in both group-living and solitary vertebrates (Whiten & van de Waal, 2018;

74 Penndorf & Aplin, 2020; Tóth et al., 2020; Webster, 2023). For example, young
75 individuals of the group-living wild meerkat *Suricata suricatta* are more likely to join
76 and interact with pre-trained demonstrators in food acquisition tasks than are adults
77 (Thornton & Malapert, 2009). In the solitary tortoise *Geochelone carbonaria*, juveniles
78 succeed in a navigation task only when they previously observed a solution by a
79 conspecific (Wilkinson et al., 2010). And tadpoles of the solitary wood frog *Rana*
80 *sylvatica* could recognize a predatory salamander when paired with predator-
81 experienced tutors (Ferrari et al., 2007). But social information about opening a novel
82 puzzle box did not affect the success rate of young group-living spotted hyenas, *Crocuta*
83 *crocuta*, because the task could be easily learned through personal trial-and-error tactics
84 (Benson-Amram et al., 2014). And young males of the great tit, *Parus major*, a social
85 songbird (Wild et al., 2024), did not copy the habitat choice of a simulated conspecific
86 (Loukola et al., 2012).
87 Social information use in young individuals of both group-living and solitary
88 species of fish is also of interest. Young females of the group-living guppy *Poecilia*
89 *reticulata* copy the mate choice of older females (Dugatkin & Godin, 1993;
90 Vukomanovic & Rodd, 2007). This use of social information may compensate for their
91 paucity of experience in evaluating male quality (Dugatkin & Godin, 1993;
92 Vukomanovic & Rodd, 2007). Juveniles of solitary sharks, moreover, perform several

93 behaviours related to a novel food task more often when paired with a pre-trained
94 demonstrator than with a shark with no previous experience (lemon shark, *Negaprion*
95 *brevirostris*, Guttridge et al., 2013; Port Jackson shark, *Heterodontus portusjacksoni*,
96 Vila Pouca et al., 2020). Although solitary fish species could benefit from social
97 information in a similar way to social species (Tóth et al., 2020; Webster, 2023), studies
98 of the juveniles of solitary species are limited to a few elasmobranchs (Guttridge et al.,
99 2013; Vila Pouca et al., 2020) and only one bony fish (European flounder, *Platichthys*
100 *flesus*; Webster & Laland, 2017). Although bony fishes include more than 30 000
101 species (Nelson et al., 2016), the ability of other juvenile solitary bony fishes is still
102 unknown. We therefore examined the use of social information by juveniles of the
103 solitary forktongue goby, *Chaenogobius annularis*.

104 *Chaenogobius annularis* is a common intertidal goby distributed around the rocky
105 coastline of Japan and southern Korea. It has a 1-year lifespan (Toyoji et al., 1984), and
106 juveniles are abundant in summer in our study area (see Methods). Since the juveniles
107 consume mainly small benthic invertebrates (Sasaki & Hattori, 1969) and live near the
108 bottom (D. Nakayama, personal observation), we first examined whether feeding on
109 novel artificial food (fish-food flakes) floating on the water surface was facilitated by
110 past training with the food. The water surface is a novel food location for the bottom-
111 feeding *C. annularis* juveniles. Since they could learn to feed on the novel food in a

112 novel food location through our training (see Results), we then examined whether the
113 presence of a juvenile that experienced the novel food task facilitates novel feeding by
114 naïve juveniles. If *C. annularis* juveniles use social information provided by an
115 experienced conspecific, juveniles paired with a demonstrator will consume the novel
116 food and show surface feeding sooner than those paired with a naïve juvenile.

117 Methods

118 Study animal and general method

119 Juvenile *C. annularis* were collected along the intertidal rocky shore in Kattoshi, on the
120 western coast of Hakodate Bay, southwestern Hokkaido, Japan (41°41′N, 140°36′E),
121 and used in our experiments during 11–14 August 2022. All fish were kept in several
122 aerated housing tanks (35.4 cm × 23.4 cm × 13.8 cm high, water ~9 cm deep) in the
123 laboratory before each experiment. After the experiments, each juvenile was measured
124 from the tip of the mouth to the base of the caudal fin as standard length (SL, 0.1 mm)
125 with callipers and then released into the field. All individuals were used once.

126 We used Tetra Kirimin fish-food flakes (Tetra, Melle, Germany; <5 mm in radius)
127 as the novel artificial food. The flakes were placed on the water surface, where they
128 floated for several hours before sinking but sometimes sunk by juvenile's moving.
129 Although we did not use a blind method on account of a lack of facilities, we observed

130 the behaviour of the juveniles with great care to minimize any bias. All statistical
131 analyses were conducted in R v. 4.1.1 software (R Core Team, 2021).

132 Experiment 1: Does past experience facilitate feeding on novel food?

133 The juveniles were assigned to one of two treatments: (1) experienced (n = 40) and (2)
134 naïve (n = 39). On the day before the trial, "experienced" juveniles were fed artificial
135 fish-food flakes three times at 4–5-h intervals in the housing tank. For the feeding, we
136 stopped the aeration of the water and then put the flakes on the water surface in the
137 centre of the tank. Juveniles were allowed to feed freely for an hour. The remaining
138 food was then removed, and aeration was turned on again. "Naïve" juveniles were
139 collected on the day of the trial and maintained without food for 5 h before the trial to
140 minimize starvation.

141 In each trial, a juvenile was introduced into a plastic container (15 cm × 10 cm × 11
142 cm high, water 7 cm deep) and allowed to acclimatize for at least 1 h. Dozens of fish-
143 food flakes were then placed on the water surface in the centre of the container, and the
144 fish was observed for 60 s to record (1) the latency (s) to begin surface feeding and (2)
145 the latency to begin underwater feeding (i.e., feeding on food that sank). There were no
146 cases where all flakes were foraged by the end of a trial.

147 SLs were 17.33 ± 3.19 mm (mean ± SD) for the experienced juveniles and 16.64 ±
148 1.78 mm for the naïve juveniles, with no significant size difference between the two

categories (Welch's *t*-test, $t = 1.198$, $P = 0.236$).

Experiment 2: Do juveniles use social information when given novel food?

The juveniles were assigned to one of two treatments: (1) a pair of one naïve and one experienced juvenile ("NE" treatment; $n = 39$ pairs, with 39 naïve), and (2) a pair of two naïve juveniles ("NN" treatment; $n = 40$ pairs, with 80 naïve). As in Experiment 1, experienced juveniles were fed artificial fish-food flakes in the housing tanks three times on the day before the trial, and naïve juveniles were maintained without food for 5 h before the trial.

The experimental procedure was similar to that in Experiment 1. In each trial, a pair was introduced into a plastic container as in Experiment 1, and we discriminated the juveniles in a container by body size. After 1-h acclimatization, dozens of fish-food flakes were placed on the water surface and the fish were observed for 60 s in both treatments to record the latencies of surface and underwater feeding. There were no cases where all flakes were foraged by the end of a trial.

For the NE treatment, to avoid any bias in the data, such as that reflecting boldness, we used all data of pairs regardless of whether the naïve juvenile fed an artificial food before or after the experienced juvenile ($n = 39$). For the NN treatment, we randomly assigned the roles of naïve and 'sham' demonstrator (e.g., Guttridge et al., 2013) in each pair. We then used the focal naïve fish's (i) latency of first feeding, (ii) latency of

surface feeding, and (iii) SL as the data of naïve juveniles in the NN treatment (n = 40).

SLs were 17.31 ± 2.46 mm (mean ± SD, n = 39) in the naïve juveniles of the NE treatment and 17.86 ± 2.76 mm in the focal naïve fish of the NN treatment. There was no significant size difference between the treatments (Welch's t-test, t = –0.932, P = 0.354).

Analyses

We first compared the frequency of feeding (either surface or underwater) and the place of first feeding (surface or underwater) between two groups of juveniles (Experiment 1, experienced vs. naïve; Experiment 2, naïve in NE vs. focal naïve in NN) by a generalized linear model (GLM) with a binomial error distribution. The response variable in each model was whether juveniles fed artificial food during the observation period (yes = 1, no = 0) or the place of the first feeding by juveniles that fed (surface = 1, underwater = 0), and the experimental variable of the four models was treatment (Experiment 1, experienced = 1, naïve = 0; Experiment 2, NE naïve = 1, NN focal naïve = 0). SL of juveniles was also included as a covariate. The treatment × SL interaction was omitted from all four models as it was not significant (P > 0.08).

We then compared the latency (s) of the first and surface feedings between juveniles (Experiment 1, experienced vs. naïve; Experiment 2, NE naïve vs. NN focal naïve) using Cox's proportional hazard models. The response variable in each model

was the latency of the first or surface feeding. The models included treatment as an explanatory variable and SL as a covariate as GLM. The four Cox's analyses were conducted by using the 'coxph' function in the 'survival' package in R (Therneau, 2021). For juveniles that did not forage during the 60-s observation period, the latency to feeding was recorded as 60 s (i.e., censored data). The proportional hazard assumption was satisfied for all models ('cox.zph' function; $P > 0.06$).

Results

Experiment 1: Experienced juveniles fed more often and sooner than naïve juveniles

Experienced juveniles fed significantly more on the novel artificial food (92.5% = 37/40) than naïve juveniles (71.8% = 28/39; Table 1a). Among those that fed, 81.1% (30/37) of the experienced juveniles and 67.9% (19/28) of the naïve juveniles fed first at the surface, with no significant difference between the two groups (Table 1a). Juvenile SL did not affect either frequency (Table 1a).

The latency of first feeding was significantly shorter in the experienced juveniles (mean ± SD = 17.5 ± 17.6 s, $n = 40$) than in the naïve juveniles (30.2 ± 21.7 s, $n = 39$) (Table 1b; Fig. 1a). Similarly, the latency of surface feeding was significantly shorter in the experienced juveniles (20.4 ± 21.0 s, $n = 40$) than in the naïve juveniles (36.6 ± 23.9

s, n = 39) (Table 1b; Fig. 1b). SL did not affect either latency (Table 1b).

Experiment 2: Naïve juveniles fed more often and sooner when they could use social information

Naïve juveniles in NE fed significantly more on the novel artificial food (79.5% = 31/39) than focal naïve fish in NN (55.0% = 22/40; Table 2a). SL did not affect the feeding frequency (Table 2a). Among those that fed, 87.1% (27/31) of the naïve juveniles in NE and 77.3% (17/22) of the focal naïve fish in NN fed first at the surface. Neither treatment nor SL had any effect on the frequency of feeding first at the surface (Table 2a). As a reference, there was no significant difference in feeding frequency between naïve juveniles in Experiment 1 (71.8%) and NE naïve juveniles (79.5%) (Fisher's exact text, P = 0.60) or between naïve juveniles in Experiment 1 and NN focal naïve juveniles (55.0%; P = 0.16).

Naïve juveniles in NE (n = 39) started both first feeding (mean ± SD = 29.0 ± 21.6 s) and first surface feeding (30.0 ± 22.2 s) significantly sooner than the focal naïve fish in NN (first, 40.5 ± 20.8 s; surface, 42.9 ± 21.1 s, n = 40) (Table 2b; Fig. 2). SL did not affect either latency (Table 2b).

Discussion

We demonstrated the use of social information about feeding by juveniles of the solitary

goby, *C. annularis*: naïve juveniles fed on novel food (fish-food flakes) in a novel food patch (water surface) sooner when paired with an experienced conspecific than with a naïve conspecific (Experiment 2). Regardless of their sociality, young individuals benefit from observing and copying others' foraging behaviour to compensate for their lack of knowledge (Guttridge et al., 2013). The use of social information in feeding by young has been reported in various vertebrates, including solitary elasmobranchs (e.g., reviewed in Webster, 2023) and European flounder, *Platichthys flesus* (Webster & Laland, 2017). Our study is the second report of this among juvenile solitary bony fishes. Since *P. flesus* (Pleuronectiformes) and *C. annularis* (Perciformes) differ at the order level, our results suggests that this ability might be widespread among juvenile solitary fishes.

Juveniles of *C. annularis* also used personal information about food. In Experiment 1, their feeding on novel food was facilitated by past experience. If we consider the difference in rearing period between experienced juveniles (1 day) and naïve juveniles (4–5 h) before the trial, greater success of feeding among experienced juveniles might be related to the difference in hunger level or motivation to feed. However, various young animals can succeed in a novel food task through both trial and error and social learning (Gosset & Roeder, 2001; Schnoell & Fichtel, 2012; Noble et al., 2014; Biondi et al., 2015). For example, hatchery-reared juveniles of the Atlantic salmon *Salmo salar*

242 with no experience of natural prey develop foraging skills and increase consumption of
243 these prey after sequential encounters (Reiriz et al., 1998). Juvenile lemon sharks,
244 *Negaprion brevirostris*, could learn a novel food patch through both their own trial-and-
245 error and social learning (Guttridge et al., 2013). Heyes (2012) has pointed out that
246 social learning might reflect general learning performance, since social cues are a form
247 of environmental cue. As *C. annularis* juveniles learned a novel food and a novel food
248 patch through both their own trial-and-error and social information use, our results align
249 with Heyes's claim.

250 The relative importance of personal and social information to *C. annularis* juveniles
251 is still unclear. Although juveniles often use social information more than personal
252 information when searching for food resources (Penndorf & Aplin, 2020), they ignore it
253 under some circumstances. For example, young Norway rats (*Rattus norvegicus*) in a
254 highly variable environment are less likely to copy the food choice of others than those
255 in a relatively stable environment (Galef & Whiskin, 2004). Juvenile minnows
256 (*Phoxinus phoxinus*) use social information on food location only when there is a
257 predation risk (Webster & Laland, 2008). For juvenile fish, whatever information is
258 used, effective food acquisition is important, because growth brings advantages such as
259 developing the ability to escape (Bishop & Brown, 1992) and avoiding gape-limited
260 predation (Nilsson & Brönmark, 2000; Feary et al., 2009). Juvenile fish therefore often

261 show more active food search behaviours than adults (Laland & Reader, 1999). Thus, *C.*
262 *annularis* juveniles might use both personal and social information according to
263 conditions (Laland, 2004) to maximize success in food acquisition.

264 Our results could also contribute which cues from the environment intertidal gobies
265 use. White and Brown (2015) showed that two species of rocky intertidal gobies use
266 visual landmarks to orientate to the location of a reward. Kłosiński et al. (2022) reported
267 that the monkey goby, *Neogobius fluviatilis*, shows antipredation behaviour when
268 detecting a damage-released alarm cue from the gudgeon *Gobio gobio*. Our results show
269 that *C. annularis* juveniles can gain social information from conspecifics, although how
270 they acquire it (e.g., visually, chemically) is still unclear. Thus, gobies can at least use
271 cues from physical attribute, heterospecifics, and conspecifics. Although social
272 information use has been examined mainly in group-living freshwater fishes (e.g.,
273 guppies), since intertidal habitats are physically complex (Suárez-Rodríguez et al.,
274 2023) and have high densities of diverse fishes (Silberschneider & Booth, 2001;
275 Murase, 2013; Andrades et al., 2018), intertidal fish might use various types of
276 information for adaptive decision-making beyond the group- and solitary-living
277 boundaries.

278 Although juveniles of both group-living and solitary species might benefit from
279 social information, examination among solitary species is taxonomically skewed:

common in fish, reptiles, and amphibians, but uncommon in mammals and birds (Allen, 2019; Webster, 2023). This makes it difficult to discuss the generality of social information use in solitary juveniles. One of the reasons for the lack of study in mammals and birds is that even in species with solitary adults, juveniles receive parental care (Galef & Laland, 2005). However, since the period or intensity of care varies in these taxa, including no care in the Megapodiidae (incubator birds) (Jones & Birks, 1992) and only 4 days' care by the hooded seal *Cystophora cristata* (Perry & Stenson, 1992), it is possible to study juvenile mammals and birds with weak sociality. Investigation is required to reveal the use of social information in juveniles of socially diverse animals.

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Table 1 Results of Experiment 1 analysed by (a) a generalized linear model (GLM) with a binomial error distribution and (b) Cox's proportional hazard model.

(a) GLM	Coefficient	SE	*t*	*P*
Whether juveniles fed on artificial food in a trial (*n* = 79)				
Intercept	0.863	2.343	0.369	0.713
Treatment	1.575	0.704	2.238	0.025
SL	0.004	0.139	0.031	0.976
Whether juveniles fed at the water surface first (*n* = 65)				
Intercept	–3.760	2.781	–1.352	0.176
Treatment	0.709	0.602	1.178	0.239
SL	0.272	0.168	1.625	0.104

(b) Cox	Coefficient	SE	*z*	*P*
Latency of first feeding (*n* = 79)				
Treatment	0.685	0.254	2.694	0.007
SL	0.067	0.047	1.436	0.151
Latency of surface feeding (*n* = 79)				
Treatment	0.800	0.275	2.909	0.004
SL	0.079	0.048	1.645	0.100

SL (standard length) is an index of body size; bold values indicate $P < 0.05$.

437 Table 2 Results of Experiment 2 analysed by (a) a generalized linear model (GLM) with

438 a binomial error distribution and (b) Cox's proportional hazard model.

(a) GLM	Coefficient	SE	*t*	*P*
Whether juveniles fed on artificial food in a trial (*n* = 79)				
Intercept	0.579	1.725	0.336	0.737
Treatment	1.143	0.510	2.239	0.025
SL	–0.021	0.095	–0.223	0.823
Whether juveniles fed at the water surface first (*n* = 53)				
Intercept	–4.582	3.485	–1.315	0.189
Treatment	0.735	0.764	0.962	0.336
SL	0.341	0.207	1.644	0.100

439

(b) Cox	Coefficient	SE	*z*	*P*
Latency of first feeding (*n* = 79)				
Treatment	0.721	0.287	2.518	0.012
SL	0.038	0.051	0.758	0.449
Latency of surface feeding (*n* = 79)				
Treatment	0.827	0.308	2.841	0.004
SL	0.055	0.054	0.292	0.292

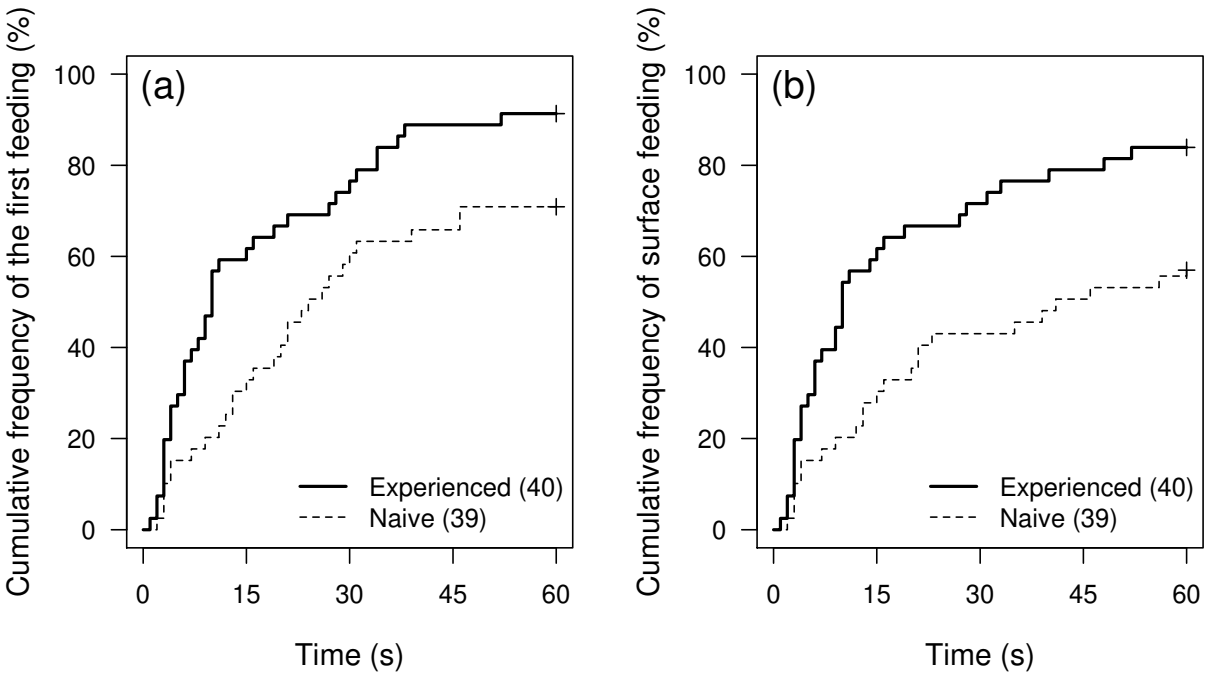
440 SL (standard length) is an index of body size; bold values indicate $P < 0.05$.

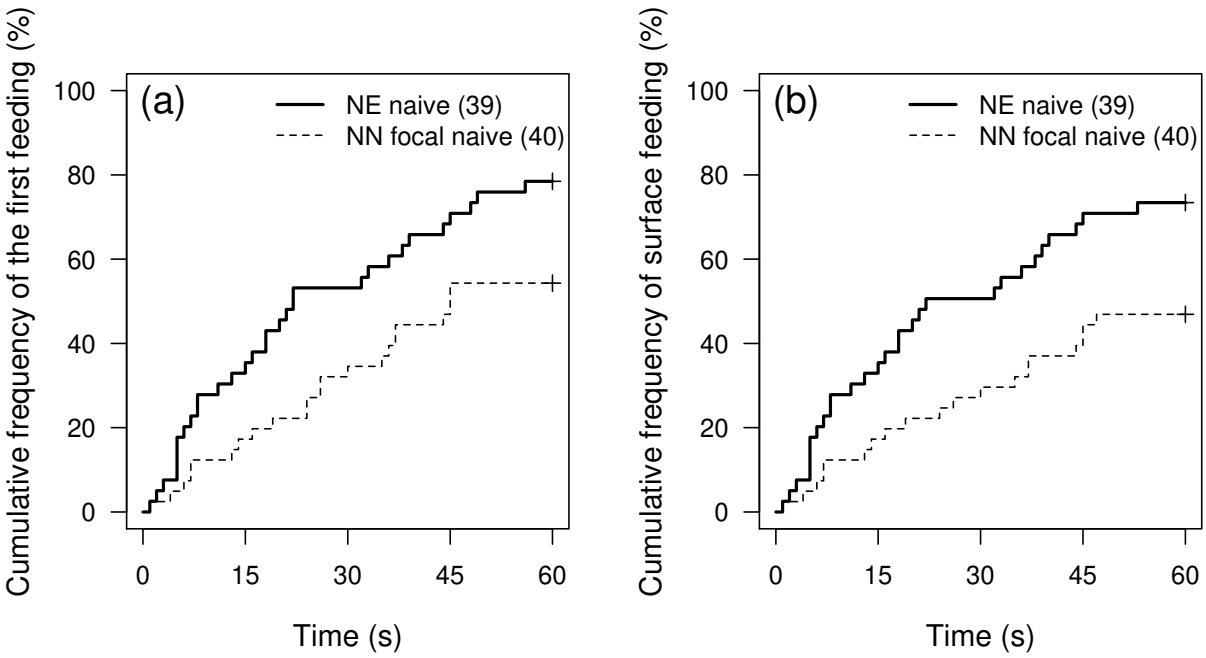
441

Figure legends

Fig. 1 Cumulative frequencies of (a) first feeding and (b) surface feeding by naïve and experienced juveniles in Experiment 1. Curves in both figures differed significantly from each other (see Table 1b). Numbers in parentheses indicate sample size.

Fig. 2 Cumulative frequencies of (a) first feeding and (b) surface feeding by naïve juveniles in NE treatment and focal naïve juveniles in NN treatment in Experiment 2. Naïve juveniles could use social information from an experienced juvenile in NE but not in NN. The focal naïve juvenile in the paired naïve juveniles was randomly determined. Curves in both figures differed significantly from each other (see Table 2b). Numbers in parentheses indicate sample size.


(a)
Cumulative frequency of the first feeding (%)
100
80
60
40
20
0
0
15
30
45
60
Time (s)
Experienced (40)
Naive (39)
(b)
Cumulative frequency of surface feeding (%)
100
80
60
40
20
0
0
15
30
45
60
Time (s)
Experienced (40)
Naive (39)


(a)
NE naive (39)
NN focal naive (40)
Cumulative frequency of the first feeding (%)
Time (s)
0
20
40
60
80
100
0
15
30
45
60
(b)
NE naive (39)
NN focal naive (40)
Cumulative frequency of surface feeding (%)
Time (s)