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Does cleanerfish service quality depend on client value or choice options?

MARTA C. SOARES*, REDOUAN BSHARY† & ISABELLE M. CÔTÉ‡

*School of Biological Sciences, University of East Anglia, U.K.
†Institut de Zoologie, Eco-Ethologie, Université de Neuchâtel
‡Department of Biological Sciences, Simon Fraser University

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Cleaning fish mutualisms appear to be good examples of biological markets. Two classes of traders exist: cleaner fish and their fish clients, each of which supplies a commodity required by the other (ectoparasite removal and a meal, respectively). However, clients are not all treated similarly by cleaners. There is evidence that clients with choice options (with potential access to more than one cleaner) have priority of access over clients without choice options. Market theory predicts that client value (i.e. ectoparasite load) should also influence cleaning service quality. We examined the relative roles of client choice options and client value in determining the duration of cleaning interactions between bluestreak cleaner wrasse, *Labroides dimidiatus*, and their clients across three geographically distant sites. We found a lack of covariation between client choice options and gnathiid ectoparasite loads. Geographical differences in gnathiid availability altered the importance of client gnathiid load as a determinant of client inspection duration. As predicted, clients with both choice options and high gnathiid loads were inspected for longer, but this was observed only in an area with a relatively high incidence of parasitism. These correlational results suggest that the importance of client choice for aspects of cleaner fish service quality may be modulated by parasite availability.

Keywords: biological market; bluestreak cleaner wrasse; cleaning fish mutualism; client choice options verses value; gnathiid availability; inspection duration; *Labroides dimidiatus*

Cooperative interactions between individuals of different species are ubiquitous and have attracted the attention of behavioural and evolutionary ecologists for decades. Game theory models such as the Prisoner's Dilemma (Axelrod & Hamilton 1981) and Tit-for-Tat scenarios (Axelrod 1984) have been used to understand the evolution of cooperation among unrelated individuals. However, it has been difficult to apply these models to real-life situations because of their restrictive assumptions. Biological market theory is emerging as a more realistic approach to capture important aspects of cooperative interactions such as asymmetric payoff distributions among partners (Noë et al. 1991; Noë & Hammerstein 1994; Noë 2001; Bshary & Noë 2003). In particular, the theory is well suited to the many cases where cooperative individuals engage in interactions with numerous partners (e.g. grooming markets in primates: Barrett et al. 1999; Barrett & Henzi 2001, 2006; Henzi & Barrett 2002; nutrient exchange in mycorrhiza: Schwartz & Hoeksema 1998; Wilkinson 2001; rhizobia: Simms & Taylor 2002).

Biological markets are characterized by competition within trader classes over access to the partner trader class by outbidding rather than contest competition. Players are predicted to prefer partners offering the highest value, while the exchange value of commodities has to be bargained according to the market law of supply and

Correspondence and present address: M. C. Soares, Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal and Department of Zoology, University of Neuchâtel, Emile-Argand 11, 2009 Neuchâtel, Switzerland (email: MSoares@ispa.pt). R. Bshary is at the Department of Zoology, University of Neuchâtel, Emile-Argand 11, 2009 Neuchâtel, Switzerland. I. M. Côté is at the Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

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demand (Noë et al. 1991; Bshary 2001; Noë 2001). Partner choice is a key element of all biological markets (Noë & Hammerstein 1994).

Cleaning mutualisms among fish appear to be good examples of biological markets. These interspecific interactions have two classes of traders: cleanerfish and their fish clients, each of which supplies a service or good required by the other (ectoparasite removal and a meal, respectively). In general, clients that potentially have access to more than one cleaner should have priority and receive a better cleaning service than clients that do not (Bshary 2001; Bshary & Noë 2003). There is indeed evidence that such clients wait less before being inspected, are inspected for longer and are less likely to experience cheating bites by cleaners (Bshary 2001; Bshary & Grutter 2002a; Bshary & Schäffer 2002). Choice options therefore seem to determine to a large extent the cleaning service quality received by clients at cleaning stations (Bshary 2001).

However, a better cleaning service should also be given to clients of higher value. Obligatory cleaners rely virtually entirely on the ectoparasites they glean from the bodies of the many fish clients they service every day (Côté 2000). The behaviour of such cleaners should therefore depend on client ectoparasite loads. In agreement with this prediction, the duration and frequency of inspections by cleanerfish have been shown to vary with client ectoparasite load (Grutter 1995; Arnal & Morand 2001; Sikkel et al. 2004).

Bshary (2001) and Bshary & Grutter (2002b) argued that the preference for clients with the potential to choose between cleaners should be independent of the clients' quality as a food patch. Field observations confirmed that cleaners preferred to inspect clients with choice options, and that this preference was independent of client body size, which was assumed to be a reliable indicator of parasite numbers (Bshary 2001). However, the relation between body size and ectoparasite load in fish is often weak (Poulin 2000), calling into question the validity of using body size as a substitute for ectoparasite load. Under experimental conditions, cleanerfish also showed a preference for artificial clients with choice options, but all clients had similar amounts of food on them (Bshary & Grutter 2002b). In nature, cleaners must choose between clients that vary in both choice options and foraging value.

We examined the relative roles of client choice options and client value (i.e. the number of parasitic gnathiid isopods on a client, simply referred to as gnathiid load) in influencing the duration of inspections by the bluestreak cleaner wrasse, *Labroides dimidiatus*, on its fish clients. *Labroides dimidiatus* is the most ubiquitous cleanerfish in the Indo-Pacific (Randall 1958). Inspection duration is a parameter that incorporates several components of cleaning service quality. The duration of any inspection is limited by the partner who decides to terminate first, which can be either the cleaner or the client. Clients often terminate inspections in response to cleaner fish cheating (Bshary & Grutter 2002a), while cleaners may be particularly likely to terminate an inspection if the client represents a food patch of low quality. Duration is thus a parameter that reflects service quality by cleaners as well as client needs. Client needs should be strongly correlated with their gnathiid load. From a cleaner's perspective, however, service quality and thereby inspection duration could be influenced by client gnathiid loads (and hence client needs) and by client choice options.

First, we tested whether clients with both choice options and high gnathiid loads were inspected by cleaner wrasses for longer than those with both no choice and low parasite loads. Second, we examined whether inspections by cleaners of clients with high gnathiid loads and no choice were longer than those of clients having choice options but low gnathiid loads, thereby establishing the relative importance of the two parameters.

METHODS

Study Sites

We carried out the study at three sites within the distribution range of *L. dimidiatus*: Ras Mohammed National Park (28°10′N, 34°56′E) in the Egyptian Red Sea, Hoga Island (5°43′S, 125°80′E) in southwest Sulawesi, Indonesia, in the Indian Ocean and the Pacific island of Guam (13°28′N, 144°47′E) in the Marianas Archipelago.

Behavioural observations in Egypt were carried out on patch reefs in Mersa Bereika, a protected bay within the Ras Mohammed National Park, during May–July 1998 and May–July 1999. Fish collections for ectoparasite enumeration were made at depths of 3–10 m between 18 and 24 November 2002. This site had lower coral cover, fish abundance and fish diversity than the other two sites. In Indonesia, both behavioural data and fish for parasite counts were collected at a site known as 'Buoy 2' off the west coast of Hoga Island between 1 and 21 August 2002 at depths of 3–17 m. This fringing reef had intermediate coral cover but high fish diversity and abundance. In Guam, observations and fish collections were carried out from 11 May to 3 June 2003 on the slope of the reef adjacent to Gun Beach on the west coast of the island, at depths of 3–15 m. The reef was characterized by high coral cover and intermediate diversity and abundance of reef fishes.

All observations of cleaning stations were made prior to the collection of fish for ectoparasite assessment.

Behavioural Observations

We observed adult bluestreak cleaner wrasses (total length > 8 cm) in situ while diving or snorkelling between 0700 and 1700 hours. Observations were made on 20 individual cleaner wrasses in Egypt, 22 in Indonesia and 19 in Guam. At each site, cleaning stations were selected haphazardly across the reef. In Egypt, during 1998, each cleaner was observed six times for 30 min each, and in 1999 each cleaner was observed on eight separate occasions for 60 min each. In Indonesia, each cleaner was observed for 15 min on three separate occasions. In Guam cleaners were observed once each for 30 min. During each observation period, we recorded the species of each client visiting the cleaning station, as well as the duration (s) of each inspection.

Ectoparasite Assessment

Ectoparasite loads were assessed for 70 individuals (16 species) in Egypt, 55 individuals (15 species) in Indonesia and 47 individuals (17 species) in Guam. All specimens were collected between 0700 and 1200 hours and were captured where behavioural observations were made. Species at each location were chosen because of their relatively high abundance and to represent a wide variation in visit frequency to cleaning stations. The methods used to quantify ectoparasites were similar to those reported by Sikkel et al. (2004). Individual fish were herded into a barrier net, caught with a hand net and then quickly transferred into hermetically sealed plastic bags filled with sea water. In the laboratory, the live fish were placed into individual containers with a variable amount of sea water and two or three drops of clove oil to induce anaesthesia. Fish were then transferred into individual freshwater baths for 10 min, during which we gently brushed their entire body surface while the fish were immobile. Fish were placed in sea water containers to recover and then released at their capture location after being identified (species) and measured ($\pm$1 mm, total length). All fluids were filtered with a plankton net (100 μm mesh size), and ectoparasites were preserved in 70% alcohol. We later counted the gnathiid isopod larvae, the usual targets of cleaner wrasse predation (Grutter 1997, 2002; Grutter & Poulin 1998; Bansemer et al. 2002), using a binocular microscope.

Ethical Note

Permits for the Egyptian part of the study were granted by the Egyptian Environmental Affairs Agency (EEAA) in Cairo. For Guam and Indonesia, the work was carried out under the auspices of the University of Guam Marine Laboratory and the nongovernmental organization Operation Wallacea, respectively. We tried to minimize as much as possible stress and other negative effects on fish during assessment of gnathiid loads. Captive fish were first kept in large plastic bags with considerable amounts of sea water to prevent suffocation. Few fish were collected (average: five individuals) per sampling period to minimize the time between capture, processing in the laboratory and release. The time elapsed between capture and release varied between less than 30 min (in Guam) to 3 h (in Indonesia). We chose the freshwater bath method of parasite extraction because it is thought to result in less skin irritation and usually entails a lower rate of mortality than alternative methods (e.g. dilute formalin solution; Sikkel et al. 2004). Mortality of captured fish was relatively low (24 of 172 individuals collected). After the parasite removal procedure, fish were placed in sea water-filled containers to recover for a minimum of 10–15 min. Full recovery was deemed to have occurred when the fish were swimming actively.

We could not examine the long-term effects of the parasite extraction procedure on the behaviour and survival of released fish because the fish were not marked; however, we did carry out focal observations (10 min long) on a small number of individuals of a variety of species at each location upon release. All fish appeared to behave normally and territorial fish appeared to reintegrate into their territories easily. Individuals with recognizable body marks (e.g. scars) were also sighted during dives on subsequent days (up to 3 days later).

Statistical Analysis

We examined the importance of client value choice and options for the duration of cleaning by bluestreak cleaner wrasse on specific client species. This specific aspect of service quality is easy to measure and therefore minimizes observer biases in the data sets. For each client species, mean inspection duration was obtained at each cleaning station and then averaged across all cleaning stations at a site. As an index of client value as a food source, we calculated the species-specific mean number of gnathiids. We removed from the ectoparasite data set those client species for which only one individual was sampled, as well as species that were never observed at cleaning stations (Table 1). Client species were categorized as having no choice options when they had small territories or home ranges that were unlikely to encompass more than one cleaning station. Conversely, client species with larger territories or home ranges that were likely to include more than one cleaning station were described as having choice options. This categorization was provided by Bshary & Grutter (2002a) for Egyptian client species, and for the other two sites was based on information gathered from the online database Fishbase (www.fishbase.org), field guides and extensive personal experience.

Gnathiid loads were square-root transformed to achieve normality. We examined variation in gnathiid loads between sites using a one-way ANOVA followed by post hoc Bonferroni tests, and between clients with and without choice options, with Student's *t* tests. To examine the importance of client parasite load and choice options as determinants of cleaning service quality provided by bluestreak cleaner wrasses to different client species, we used analyses of covariance (ANCOVA) with choice options as a fixed factor (two levels: choice, no choice) and gnathiid loads as a continuous covariate. We also included fish size as a covariate in these analyses. Fish size and gnathiid loads were not correlated (see Results); however, fish size could have an independent effect on cleaning duration if, for example, it takes longer for cleaners to inspect a larger fish regardless of parasite load. We therefore used total length^3 as an index of size, where mean species-specific total length was derived from fish collected for the ectoparasite assessment.

Although the ANCOVA approach could reveal the significance of the two main effects considered, it could not reveal the relative importance of these effects and allow us to test the two predictions stated at the onset. To do so, we therefore categorized client species as having

Table 1. Client fish species considered in this study, their choice options regarding access to cleaning stations, gnathiid load categories (high or low, see Methods for details) and the number of individuals collected across the three study sites

Species	Choice options	Gnathiid load	No. individuals collected
Egypt			
Acanthuridae			
Acanthurus nigrofuscus	Choice	High	6
Ctenochaetus striatus	Choice	High	2
Caesionidae			
Caesio lunaris	Choice	Low	2
Chaetodontidae			
Chaetodon fasciatus	No choice	High	6
Heniochus intermedius	No choice	Low	6
Labridae			
Thalassoma rueppellii	No choice	Low	5
Mullidae			
Parupeneus forsskali	Choice	High	5
Parupeneus macronema	Choice	High	4
Pomacentridae			
Abudefduf saxatilis	Choice	Low	2
Amblyglyphidodon leucogaster	No choice	Low	6
Chromis dimidiata	No choice	High	2
Pomacentrus trichourus	No choice	Low	5
Nimepteridae			
Scolopsis ghanam	Choice	Low	5
Serranidae			
Pseudanthias squamipinnis ♀	No choice	Low	6
Pseudanthias squamipinnis ♂	No choice	Low	6
Indonesia			
Acanthuridae			
Ctenochaetus striatus	Choice	Low	4
Zebrasoma scopas	Choice	Low	6
Chaetodontidae			
Chaetodon trifasciatus	No choice	Low	5
Mullidae			
Parupeneus barberinus	Choice	High	5
Parupeneus multifasciatus	Choice	High	4
Nemipteridae			
Scolopsis margaritifer	Choice	Low	5
Pomacentridae			
Amblyglyphidodon curacao	No choice	High	6
Chromis ternatensis	No choice	Low	6
Dischistodus melanotus	No choice	Low	4
Dischistodus perspicillatus	No choice	High	4
Scaridae			
Chlorurus pyrrhurus	Choice	Low	2
Guam			
Acanthuridae			
Acanthurus nigrofuscus	Choice	Low	5
Ctenochaetus striatus	Choice	High	3
Balistidae			
Balistapus undulatus	Choice	High	4
Chaetodontidae			
Chaetodon ulietensis	No choice	Low	2
Labridae			
Bodianus axillaris	No choice	High	3
Halichoeres hortulanus	No choice	High	4
Thalassoma hardwicke	No choice	Low	3
Thalassoma lutescens	No choice	High	5

Table 1. (*continued*)

Species	Choice options	Gnathiid load	No. individuals collected
Pomacentridae			
Abudefduf sexfasciatus	Choice	Low	5
Abudefduf vaigiensis	Choice	Low	2
Plectroglyphidodon lacrymatus	No choice	High	2
Pomacentrus vaiuli	No choice	Low	2
Serranidae			
Cephalopholis urodeta	Choice	Low	3

high or low gnathiid loads, based on whether they were above or below the median overall gnathiid load, respectively, for their sampling location. Hence, we had four categories of clients that varied in choice options (choice/no choice) and gnathiid loads (low/high; Table 1), allowing us to test the two predictions stated earlier. We then carried out simple comparisons of all four categories of clients, using one-way ANOVAs, followed by Bonferroni post hoc tests. All tests are two tailed.

RESULTS

Gnathiid Loads

Gnathiid numbers varied significantly between sites (one-way ANOVA: $F_{2,36} = 7.16$, $P = 0.002$; Fig. 1), with fishes in Guam having significantly higher gnathiid loads than those in Egypt and Indonesia (Bonferroni post hoc tests: Egypt versus Guam: $P = 0.002$; Indonesia versus Guam: $P = 0.04$). There was no difference in gnathiid load between clients from Egypt and Indonesia (Bonferroni post hoc test: $P = 1.00$). Client gnathiid loads did not differ on clients with and without choice options, either overall (Student's t test: $t_{37} = -0.37$, $P = 0.71$) or at any of the individual sites (Egypt: $t_{13} = -1.20$, $P = 0.25$; Indonesia: $t_9 = -0.77$, $P = 0.46$; Guam: $t_{11} = 0.36$, $P = 0.72$). Client gnathiid load was significantly correlated with fish size when all three sites were combined (Pearson correlation: $r_{39} = 0.34$, $P = 0.04$), but not at any individual site (Egypt: $r_{15} = -0.15$, $P = 0.56$; Indonesia: $r_{11} = 0.53$, $P = 0.09$; Guam: $r_{13} = 0.41$, $P = 0.17$).

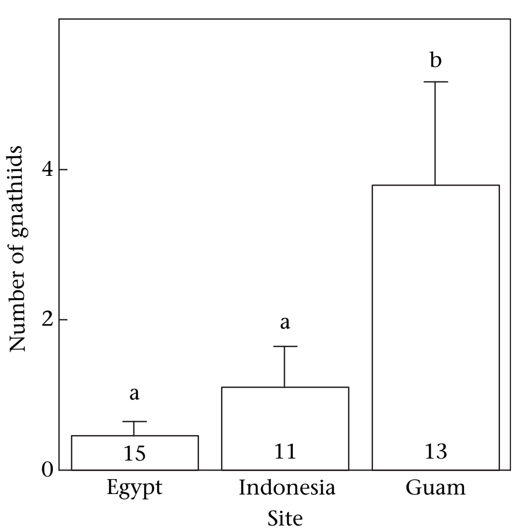

Figure 1. Client fish gnathiid load at the three study sites. Means are shown +1 SE. Sample sizes (number of client species) are given in the bars. Means with different letters were significantly different from each other in Bonferroni post hoc tests ($P < 0.05$).

Inspection Duration

In Egypt and Indonesia, inspection duration did not vary with client choice options (ANCOVA: Egypt: $F_{1,11} = 2.45$, $P = 0.15$; Indonesia: $F_{1,7} = 0.06$, $P = 0.81$) or gnathiid loads (Egypt: $F_{1,11} = 0.65$, $P = 0.44$; Indonesia: $F_{1,7} = 0.29$, $P = 0.61$). By contrast, in Guam cleaners tended to inspect clients with choice options for longer than clients without choice options ($F_{1,9} = 4.81$, $P = 0.056$) and inspection duration increased with gnathiid loads ($F_{1,9} = 5.82$, $P = 0.04$). Inspection duration was not related to fish size at any location ($F < 2.67$, $P > 0.14$ in all cases).

Significant differences in inspection durations across the four categories of clients were detected in Guam alone (one-way ANOVA: $F_{3,9} = 4.36$, $P = 0.04$; Fig. 2). Inspection duration on clients with both choice options and high gnathiid loads was significantly higher than on clients without choice options and lower gnathiid loads (Bonferroni post hoc tests: $P = 0.04$). However, clients with choice options and low gnathiid loads were inspected for a similar length of time as clients with no choice options and higher gnathiid loads (Bonferroni post hoc test: $P = 1.00$). There were no differences in inspection duration between client categories in Indonesia or in Egypt.

DISCUSSION

We found that inspection duration varied with both client choice options and parasitic gnathiid loads but this variation changed geographically. Geographical differences in gnathiid availability may be responsible for the different patterns. In areas of low gnathiid availability, such as Egypt and Indonesia, client gnathiid loads did not affect inspection duration. By contrast, where there was a higher incidence of gnathiid infestation, such as in Guam, gnathiid load on clients became important for inspection duration, as did client choice options. Our correlational study therefore suggests that the importance of client choice for service quality might be modulated by parasite availability.

The link between client choice options and gnathiid load of clients had not been previously examined. Bshary & Noë (2003) suggested that clients with choice options

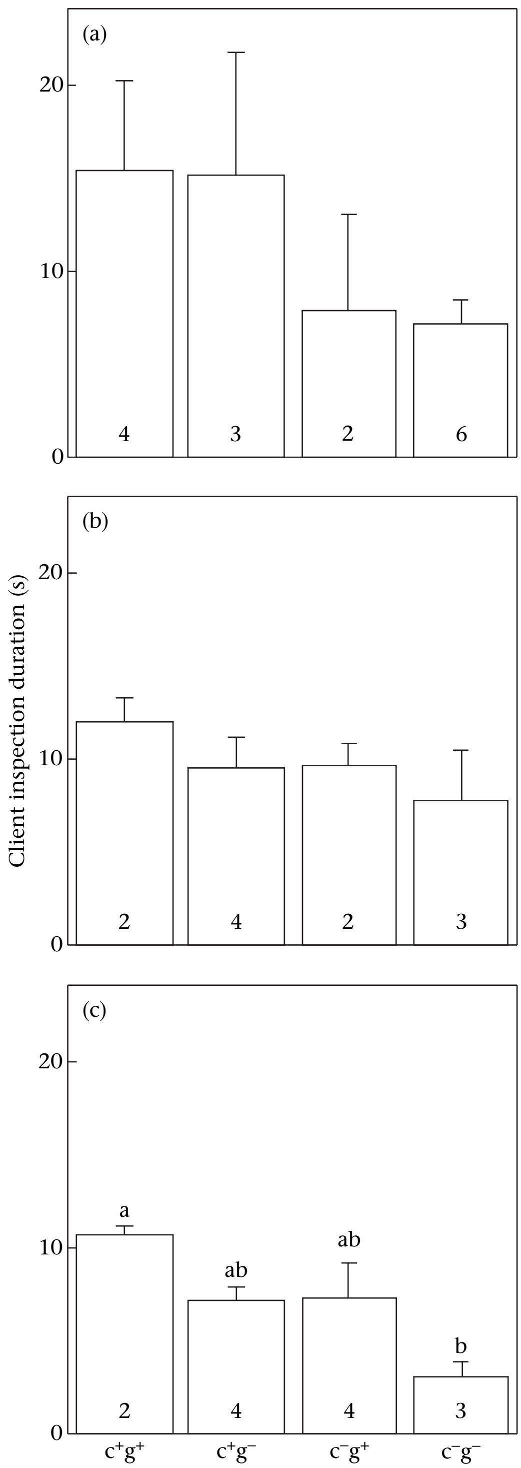

Figure 2. Duration of inspection (s) by bluestreak cleaner wrasse on clients with varying choice options and gnathiid loads across sites: (a) Egypt, (b) Indonesia and (c) Guam. Means are shown +1 SE. Sample sizes (number of client species) are given in the bars. Means with different letters were significantly different from each other in Bonferroni post hoc tests ($P < 0.05$). c^+g^+: with choice options and high gnathiid loads; c^+g^-: with choice options and low gnathiid loads; c^-g^+: no choice options and high gnathiid loads; c^-g^-: no choice options and low gnathiid loads.

could be more vulnerable to ectoparasite infestation than clients with smaller home ranges without choice of cleaners, if either increased movement causes higher infestation rates or clients with choice options frequent cleaning stations less often. Higher ectoparasite loads would therefore make these clients with access to multiple cleaning stations more valuable from a cleaner's foraging perspective (Gorlick 1984; Grutter 1995, 2001; Arnal & Morand 2001). Our findings do not support these possibilities but suggest instead an absence of covariation between client choice options and gnathiid load which gave scope for both factors to be independently important in determining cleaning service quality.

Our first prediction that clients with both choice options and high gnathiid loads should be inspected by cleaner wrasses for longer than those with both no choice and low parasite loads was confirmed only in Guam. We had also predicted that if client gnathiid load was relatively more important than choice options, clients with high gnathiid loads and no choice should be preferred over those with choice options and few gnathiids. The converse pattern would have suggested a relatively greater importance of choice options. The duration of inspection for these two categories of clients did not differ, suggesting that, in Guam at least, gnathiid availability and client choice options may be equally important determinants of cleaning service quality and hence inspection duration.

The effect of ectoparasite availability on the relative importance of choice options and gnathiid loads for cleaning service quality is not surprising. When gnathiid availability is high, those clients with the most gnathiids may be particularly valuable, and providing a good service to clients with choice options makes their return likely (Bshary & Schäffer 2002). However, in areas with few gnathiids, there may be little scope for cleanerfish to discriminate between clients on the basis of parasite loads. In such locations, cleanerfish success could depend only on providing a good cleaning service to clients with choice options to ensure the return of these customers (Bshary & Noë 2003). Prolonged interactions with these clients could increase the overall conspicuousness of cleaners, further increasing clientele. A nonsignificant ($P = 0.15$) tendency for choice options alone to be important was observed in Egypt (Fig. 2), where fish had the lowest mean gnathiid load (Fig. 1). A larger sample size, or the addition of site(s) with even smaller gnathiid loads than Egypt, may have allowed us to detect this pattern.

A potentially confounding variable could be geographical variation of cleanerfish foraging preferences. Although many cleanerfish, including *L. dimidiatus* from several locations, have been shown to forage selectively on gnathiid isopods (Grutter 1994, 2001; Arnal & Côté 2000; Arnal & Morand 2001), the foraging preferences of cleanerfish are known to vary geographically (Grutter 1994, 1997; Cheney & Côté 2003). Significant intersite differences may exist in the availability of preferred ectoparasites but we could not detect these in the absence of detailed site-specific dietary information. Geographical variation in data quality could also have affected the results. For example, the behavioural observations in Egypt predated the collection of fish for parasite enumeration by 2–3 years, but at the other two sites, behaviour and parasite data were collected simultaneously. Nevertheless, the lack of importance of gnathiids and choice options observed in Egypt was similar to that of Indonesia, the other low-parasite site, but dissimilar to the pattern observed in Guam, the high-parasite location. Including the Egyptian data, in spite of its shortcomings, adds some support to our interpretation.

There is growing evidence that spatial and temporal variability in cleanerfish behaviour is linked to variation in ectoparasite availability (Grutter 1997; Bansemer et al. 2002; Côté & Molloy 2003; Sikkel et al. 2004; Cheney & Côté 2005). Our results suggest that both client choice options and gnathiid loads are correlated with cleaning duration in an area with a relatively high incidence of gnathiids, whereas at low gnathiid availability neither seemed to be important. The generality of this pattern needs to be verified by considering a wider range of sites that vary in ectoparasite availability. Our prediction for such a larger comparative study is that with increasing ectoparasite (gnathiid) abundance, client value will become relatively more important for cleaner fish service quality, as reflected by interaction duration, whereas the impact of choice options should diminish. From a cleanerfish perspective, these parasite density-dependent decisions will always result in the selection of partners yielding the highest profit, as predicted by market theory (Noë & Hammerstein 1994; Noë 2001).

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