Behavioural interdependence in a shrimp-goby mutualism

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Abstract

The partnership between non-burrowing gobiid fishes and alpheid shrimps is one of the most remarkable interspecific mutualisms currently recognised in behavioural biology. The shrimp rely on tactile and chemical cues from their goby partners to warn them of approaching predators. In return, the shrimp construct and maintain the burrows which provide shelter for the goby. Although aspects of this relationship have been well studied, less is known about the interdependence of the two species' activity patterns. We conducted field observations of an obligate shrimp-goby mutualism, *Ctenogobiops feroculus* and its common shrimp partner *Alpheus djeddensis*. We found that individual gobies were consistent in their activity levels relative to conspecifics over a 3-day period but were not consistent in terms of the time allocated to vigilance. Both the activity and the vigilance behaviour of the goby directly correlated with the behaviour of their shrimp partners; shrimp with a more active partner were themselves more active, and visibility of the shrimp increased as vigilance time increased. By quantifying the interactions between the two species, we have gained greater insights into the mechanistic underpinnings of these complex behavioural interactions.

Introduction

It is well established that individual animals not only show consistent patterns of behaviour, but are also consistent in their levels of behavioural plasticity (Wilson *et al.*, 1994; Gosling & John, 1999; Sih *et al.*, 2004). However, questions remain as to the ultimate functional consequences of behavioural variation between individuals, especially for social animals. Individuals from the same populations differ significantly in their level of behavioural plasticity, with some individuals being consistently more or less plastic than others, and thus animals may be constrained in the behaviours they can perform (Sih & Bell, 2008; Wolf, van Doorn & Weissing, 2008; Coppens, de Boer & Koolhaas, 2010; Dingemanse & Wolf, 2010). Therefore, there likely exists an evolutionary trade-off between being consistent in behaviour, at the risk of behaving suboptimally, and being highly plastic (Nussey, Wilson & Brommer, 2007; Chevin, Lande & Mace, 2010).

Mutualisms by definition are characterised by net benefits to both participants (Boucher, 1988). However, the interests of both parties are not always aligned, and the pressure on each participant to obtain maximum benefits is high, which may ultimately lead to selfish behaviour by one or both partners (Heil *et al.*, 2014). Collaboration between unrelated individuals in particular is often punctuated by incidences of 'cheating' (e.g. Bshary & Grutter, 2002). When individuals interact repeatedly within mutualisms, mechanisms such as reciprocity, punishment and reward and partner switching (Axelrod & Hamilton, 1981; Clutton-Brock & Parker, 1995; Schwagmeyer, 2014), can regulate the frequency of cheating and maintain the integrity of the relationship. Thus, individuals who are less cooperative can be policed or even excluded from the relationship, thereby enhancing the evolutionary stability of the mutualism over time (McNamara *et al.*, 2008, 2009). Previous work on cleaner fish mutualisms however, has shown that individuals differ in their propensity to cheat their mutualist partners (Wilson *et al.* 2002). This variation in behaviour at the individual level is not only a qualification for personality (i.e. consistent behaviour within and between individuals over time), suggesting that personalities may play a role in mutualist behaviour, but also provides a possible explanation as to why cheating persists as a strategy in obligate mutualisms in nature (e.g. Pellmyr, Leebens-Mack & Huth, 1996; Yu & Pierce, 1998). For instance, if certain personality types are more likely to cheat than others, these two tactics may persist due to fluctuations in frequency-dependent selection, or alternatively, represent two evolutionarily stable strategies (Wolf & McNamara, 2012).

The partnership between non-burrowing gobiid fishes and alpheid shrimps represents a unique opportunity to investigate the mechanistic basis of mutualism (for a review on shrimp-goby associations, see Karplus & Thompson, 2011). The shrimp are reliant predominantly on the goby to warn them of approaching predators, however they also benefit from an

increase in food sources provided by the goby such as ectoparasites (Jaafar, Tan & Chen, 2014) and faecal matter (Kohda *et al.*, 2017). In return, the shrimp construct and maintain the burrows that are used as shelter for the goby. Although the goby may provide a valuable service, it is likely that individual differences in behaviour may cause some gobies to 'cheat' or preferentially exploit their partners by spending little or no time in close association. Variation between methods and rates of cooperation has not yet been explored in these partnerships, and the role of both individual differences in behaviour and behavioural interdependence between partners has not yet been examined.

Here, we examine the interactions between the fierce shrimpgoby, *Ctenogobiops feroculus* and its shrimp partner, *Alpheus djeddensis,* in the field. We would assume that as these associations are considered obligatory mutualisms, individuals largely behave predictably, with all individuals showing a similar degree of behavioural plasticity in order to facilitate cooperation. In terms of personality and plasticity, obligate mutualisms are of interest as the personality of one mutualist could potentially act as an agent of selection in the other (Wolf & Weissing, 2012; Wilson *et al.*, 2014), thus the distribution of personality types is likely to not only affect the direct fitness of those participating, but also the ecology and potentially the coevolution of both species (Boucher, James & Keeler, 1982; Boucher, 1988; Lyons, 2012, 2013; Wilson *et al.*, 2014).

When mutualists engage in exploitative competition, predictable individuals are likely to provide higher quality resources to their partners than unpredictable ones, as partners can more reliably punish exploitative partners or reward cooperative ones. However, the extent to which mutualist behaviour is influenced by personality traits of both partners is yet to be examined. Here, we aim to investigate this question by examining the behaviour of both gobies and shrimps in terms of consistency and to determine whether pairs synchronise their behaviour as a potential way of maximizing payoffs.

Materials and methods

Study site and species

Observations were conducted at One Tree Island Research Station (23°30′30″S 152°05′30″E) on the Great Barrier Reef, Australia, in April 2014. The field site was located in the shallow gutter area (depth 1–2 m) adjoining the island, where partnerships between *Ctenogobiops feroculus* and *Alpheus djeddensis* were in high abundance (0.5–1 pair per square metre) and sightings of different mutualistic goby or shrimp species were rare. As both shrimp and gobies tend to be most active around the middle of the day (Cummins 1979, personal observation), partnerships were filmed for 30 min a day using digital cameras placed approximately 30 cm from the burrow entrance (Panasonic Lumix DMC-TS4, GoPro HD Hero) between 11 AM and 2 PM. Most partnerships were filmed on 3 consecutive days, however if neither partner emerged after 30 min on a trial day, the trial was not included and the partnership was filmed the following day. Weather conditions across the trial period were consistently sunny and both tidal conditions and time to high tide were recorded each day. In total, 26 partnerships of *C. feroculus* and *A. djeddensis* were used for subsequent analysis. Care was taken to avoid any burrows with multiple entrances or multiple gobies, and although we cannot rule out the possibility that multiple gobies relied on the same burrow, typically burrows had a single entrance and single goby occupant.

Behavioural analysis

Individual behaviours of both the shrimp and the goby in each burrow were analysed using Jwatcher software (http://www.jwatcher.ucla.edu). Shrimp behaviour outside of the burrow was limited to two main tasks; excavating or foraging. Excavation involved transporting sediment either in or out of the burrow entrance and accounted for a majority of the time spent whilst outside the burrow (Thompson, 2004; Karplus & Thompson, 2011). Therefore, we defined shrimp activity as the frequency with which the shrimp emerged from and then retreated into the burrow as this gave a good indication of excavation effort. Time spent outside the burrow has previously been considered vital to the shrimp as this was thought to be when they perform a large proportion of their foraging behaviour, with previous studies showing marked reductions in foraging activity and growth rates in shrimp deprived of their goby partners (Thompson, 2003; Nelson, 2005). In this case, foraging entailed picking at the substrate and consuming either algae or other material. However, recent work by Kohda *et al.* (2017) has shown that gobies provide a food source to shrimp through their faeces inside the burrow, suggesting time spent outside the burrow may not be as necessary to foraging effort as first thought. We therefore quantified simply the time spent visible for the shrimp, combining all instances where it was outside the burrow.

Individual goby behaviour was broadly categorised into three main states in reference to the benefit to the shrimp partner; being either positive, negative or neutral (i.e. with no obvious advantage or disadvantage). First, vigilance behaviour was defined as any instance in which the goby was positioned at the entrance of the burrow and within tactile range of the shrimp. Preliminary observations determined that shrimp would not exit the burrow unless a part of the gobies body (most often the tail) was physically on or within the burrow entrance, therefore our second measurement, selfish behaviour, was defined as any instance in which the goby was away from the burrow and therefore out of tactile range of the shrimp. This included instances where the goby was both visible and out of sight of the camera. Third, hiding behaviour was quantified as the amount of time the goby spent fully within the burrow and was considered a neutral behaviour to the shrimp. Additionally personality traits of the goby included activity levels and boldness. Activity was determined from the number of locomotory movements an individual made. Gobies generally exhibit saltatory swimming behaviour, characterized by quick movements and longer stationary periods, each change in position or instance of movement was counted as a change in behaviour. Following previous studies of *in situ* personality assays

(Krause *et al.*, 1998; Briffa, Rundle & Fryer, 2008), we used the time to emergence of the goby after the initial camera placement as a measure of boldness. Cameras were only ever deployed when the goby was positioned at the burrow entrance to ensure the goby was present for the trial and also to subsequently measure their startle response, characterised by a rapid retreat into the burrow (Karplus & Thompson, 2011).

Statistical analysis

We used an exact binomial test to compare emergence order between the goby and the shrimp. In instances where either a shrimp or goby never emerged during a session, these individuals were given a maximum emergence time of 1800 s for further analysis. We then used intraclass correlation coefficient (ICC) analysis in R using the 'irr' package (https://cran.r-project.org/web/packages/irr/irr.pdf) to determine the relative consistency of individual level behaviour for each behavioural trait (Shrout & Fleiss, 1979; McGraw & Wong, 1996). Comparisons between the goby and shrimp behaviour were made again using Spearman rank correlation tests. Where behaviours were not repeatable, comparisons among species were made separately for each day.

Results

As expected, the goby emerged before the shrimp in all trials after the initial camera placement (exact binomial test, $P < 0.001$). Emergence time for both the goby and shrimp varied greatly with the goby emerging on average 165.42 s ($\pm$370.09 SD) after camera placements, compared to the shrimp, 770.28 s ($\pm$772.21 SD). Adjusting for emergence time, gobies subsequently spent more time out of the burrow than their partner shrimps (Fig. 1). Emergence time after initial
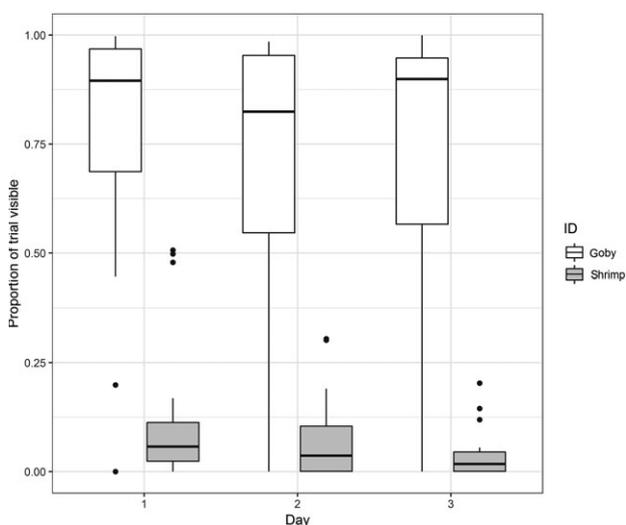

Figure 1 The proportion of time (from each 30 min trial) spent out of the burrow per day for the goby and shrimp. Shown are the median and the interquartile range for $n = 26$ gobies and $n = 26$ shrimp.

Table 1 Intraclass correlation coefficient analysis (including 95% confidence intervals and significance) assessing individual consistency across the three trial days

Measurement variable	ICC (CI 95%)	*P*-value
Goby		
Emergence time	0.015 (−0.89 to 0.56)	0.467
Time visible	0.145 (−0.64 to 0.59)	0.310
Activity	0.537 (0.11 to 0.77)	0.010
Time selfish	0.059 (−0.81 to 0.55)	0.416
Time vigilant	0.165 (−0.6 to 0.6)	0.288
Proportion vigilant	0.219 (−0.5 to 0.62)	0.220
Shrimp		
Emergence time	0.488 (0.02 to 0.75)	0.022
Activity	0.054 (−0.81 to 0.55)	0.421
Time visible	0.052 (−0.81 to 0.54)	0.422

camera placement was not repeatable at the individual level for gobies (Table 1). When adjusting for goby emergence time, individual shrimp were consistent in the time it took for them to emerge after their goby partner (Table 1).

Gobies were consistent in their level of activity, both overall and when adjusting for time spent visible (ICC(3,k) = 0.537, $P = 0.01$; and ICC(3,k) = 0.453, $P = 0.01$ respectively). Thus, some gobies were consistently more active than others. Gobies were not consistent in the type of behaviour they performed however, with neither the absolute time spent being selfish or vigilant, nor the proportions of time spent selfish or vigilant being repeatable across days (Table 1).

Goby activity was significantly correlated with both shrimp emergence time (Spearman rank correlation test: $r^2 = 0.263$, $P < 0.001$) and shrimp visibility (Spearman rank correlation test: $r^2 = 0.332$, $P < 0.001$). The more active the goby, the more likely its shrimp would emerge sooner and be more visible overall. Shrimp visibility also increased as a function of goby vigilance (Spearman rank correlation test: $r^2 = 0.468$, $P < 0.001$).

Discussion

This study has provided some of the first empirical evidence of behavioural interdependence and individual level consistency in behaviour in shrimp-goby mutualistic interactions. Individual gobies were consistent in their level of activity but were not consistent in the amount of time that they spent performing selfish behaviours (e.g. foraging, looking for mates) or being vigilant. Thus it appears, that differences in behavioural tendency do not predict the value or reliability of the partner. Shrimp behaviour was closely related to that of their goby partners however. Shrimp visibility, and thus activity outside of the burrow increased as goby vigilance behaviour increased, as expected.

Individual gobies were consistent in their levels of activity across the 3 days. By contrast, neither time spent being selfish nor vigilant was consistent at the individual level or correlated with individual activity levels. Consistency in activity is a frequently observed personality trait among animals (Sih *et al.*, 2004; Michelangeli, Wong & Chapple, 2016),

whereas vigilance behaviour and selfish behaviour as we define it here, although measures of partner quality, are both likely to be highly context specific. For instance, being at or away from the burrow is dependent on numerous factors such as the presence and behaviour of predators, of nearby conspecifics, and of the shrimp that cohabits with the goby. Moreover, if the goby is providing food for the shrimp through its faeces as seen in Kohda *et al.* (2017), time spent foraging, although selfish in the literal sense, would have the secondary benefit of producing more faeces for the shrimp to consume. These factors, along with internal state of both mutualists all likely influence the time budget allocations of the gobies in respect to guarding or leaving the burrow, and due to the potential secondary benefits of foraging for the goby and the shrimp, the likelihood of cheating in this system would be greatly diminished due to the relatively small costs involved when either partner acts selfishly.

Unlike selfish or guarding behaviour, activity as we measure it here, is event based, rather than a time budget allocation, which may explain the difference in consistency also. Activity levels are a much more general measure of individual behaviour, and may suggest that although personality traits are present, differences in time allocation may form part of a cooperative strategy typical of obligate mutualists (Clutton-Brock & Parker, 1995), rather than a personality trait per se. Further work looking at both specific behavioural traits over a longer time period, as well as looking at the long-term cooperative behaviour of both partners will help determine whether indeed activity levels are a selective force in this system, and whether or not certain individuals adopt different strategies in regard to their partners.

As expected, gobies emerged before their partner shrimps in all trials and were far more visible throughout, thus reinforcing the notion that they play a different functional role in the partnership to the shrimps, and follow a different anti-predator strategy. Further, it appears to demonstrate that the emergence of the shrimp does indeed depend on the prior emergence of the goby. The consistency of emergence times for the shrimp, following the emergence of the goby, also seems to suggest that, for the shrimp, the process of making the decision to emerge from the burrow only begins when the goby emerges, and individual variation at least partially dictates how long the shrimp waits thereafter. The lack of consistency in emergence times for the gobies was surprising, but like the other behaviours mentioned above, emergence is likely sensitive to factors such as perceived predation threat, territoriality, the behaviour of the shrimp and the internal state of the goby. Indeed, a recent study on two species of shrimp-associating goby from the genus *Amblyeleotris*, showed faster emergence times after a disturbance and smaller flight initiation distances in areas of either high human disturbance by divers, or high environmental disturbance from wave and sediment movement (Valerio *et al.*, 2019). This finding highlights that threat sensitivity and habituation to disturbance are context specific and thus less likely to be indicative of individual behavioural variation.

Shrimp visibility was greatest in partnerships where the goby spent a high proportion of time being vigilant. Shrimps rely largely on tactile and chemical cues from the goby, therefore a goby guarding at the entrance to the burrow provides

the cues that are necessary for the shrimp to come out. Interestingly, the activity levels of the goby were also correlated with increased shrimp visibility. A possible explanation of this is the reliance on visual cues. *Alpheus rapax,* another goby-associating shrimp, has been shown to detect and react to motion, but not respond to stationary figures, suggesting a reliance on visual cues as well as tactile ones (Jaafar & Zeng, 2012). If indeed this is the case here, an increase in goby activity likely provides an additional cue signalling relative safety to the shrimp. Taken together, these potentially suggest a way of maximizing benefits for both partners, as shrimp activity outside the burrow increases foraging opportunities for the goby, and goby activity similarly allows foraging for drifting particles in the immediate environs of the burrow entrance.

The presence of both obligate and facultative species of shrimp-associating gobies provides a fascinating avenue for future work. The mutualistic association between gobies and shrimp has evolved at least twice (Thacker, Thompson & Roje, 2011; Thacker and Roje, 2011), and potentially more. Thacker *et al.* (2011) showed the first instance arose in a clade containing *Ctenogobiops, Amblyeleotris* and *Vanderhorstia* species, with the second time including other common reef genera such as *Cryptocentrus*. This study has attempted to relate the behaviour patterns of two specific partners engaged in an obligate interspecific, mutualistic relationship, and thus an exciting next step would be to explore if behavioural and strategical differences are species or lineage dependent, or if indeed there are marked differences between facultative and obligate behavioural types.

The findings reported here could be strengthened by examining not only how environmental factors influence behaviour, but also how the relationship changes across tide and time of day, across a range of temperatures, conspecific densities and predator threats, and taking into account the metabolism of the animals to provide insight to the role of internal state in shaping their interactions. More work could be done to look at distributions of behavioural types across the substrate and also the interactions between neighbouring gobies. Intraspecific competition has been shown to affect size assortment in these species (Thompson, 2005), therefore competition for holes, and mating opportunities are likely to affect behaviour also. An exciting future research focus would then be to determine whether certain personality traits are pre-adaptations or the result of coevolution with shrimp.

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Author Contributions

ALB and AJWW conceived and designed the research. ALB performed the experiments. ALB, ADMW and AJWW analysed the

data. AJWW contributed materials. ALB, ADMW and AJWW wrote the paper.

References

Axelrod, R. & Hamilton, W.D. (1981). The evolution of cooperation. *Science* **211**, 1390–1396.

Boucher, D.H. (1988). *The biology of mutualism: ecology and evolution*. Oxford: Oxford University Press. on Demand.

Boucher, D. H., James, S. and Keeler, K. H. (1982). The ecology of mutualism. *Annu. Rev. Ecol. Syst.* **31**, 5–347.

Briffa, M., Rundle, S.D. & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proc. Biol. Sci.* **275**(1640), 1305–1311. https://doi.org/10.1098/rspb.2008.0025.

Bshary, R. & Grutter, A.S. (2002). Asymmetric cheating opportunities and partner control in the cleaner fish mutualism. *Anim. Behav.* **63**, 547–555.

Chevin, L.M., Lande, R. & Mace, G.M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**(4), e1000357.

Clutton-Brock, T.H. & Parker, G.A. (1995). Punishment in animal societies. *Nature* **373**(6511), 209–216.

Coppens, C.M., de Boer, S.F. & Koolhaas, J.M. (2010). Coping styles and behavioural flexibility: towards underlying mechanisms. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365** (1560), 4021–4028. https://doi.org/10.1098/rstb.2010.0217.

Cummins, R.A. (1979). Ecology of the Gobiid Fishes Associated with Alpheid Shrimps at One Tree Reef. Doctoral dissertation, University of Sydney.

Dingemanse, N.J. & Wolf, M. (2010). Recent models for adaptive personality differences: a review. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 3947–3958.

Gosling, S.D. & John, O.P. (1999). Personality dimensions in nonhuman animals: a cross-species review. *Curr. Dir. Psychol. Sci.* **8**(3), 69–75. https://doi.org/10.1111/1467-8721.00017.

Heil, M., Barajas-Barron, A., Orona-Tamayo, D., Wielsch, N. & Svatos, A. (2014). Partner manipulation stabilises a horizontally transmitted mutualism. *Ecol. Lett.* **17**(2), 185–192.

Jaafar, Z. & Zeng, Y. (2012). Visual acuity of the goby-associated shrimp, Alpheus rapax Fabricius, 1798 (Decapoda, Alpheidae). *Crustaceana* **85**(12–13), 1487–1497.

Jaafar, Z., Tan, W. & Chen, D. (2014). Goby and shrimp associations: more than meets the eye. *Coral Reefs* **33**(3), 863–863.

Karplus, I. & Thompson, A.R. (2011). *The partnership between gobiid fishes and burrowing alpheid shrimps*: 559–608. New Hampshire: Biology of gobies. Science Publishers Inc.

Kohda, M., Yamanouchi, H., Hirata, T., Satoh, S. & Ota, K. (2017). A novel aspect of goby–shrimp symbiosis: gobies provide droppings in their burrows as vital food for their partner shrimps. *Mar. Biol.* **164**(1), 22.

Krause, J., Loader, S.P., McDermott, J. & Ruxton, G.D. (1998). Refuge use by fish as a function of body length-related

metabolic expenditure and predation risks. *Proc. R. Soc. Lond. Series B. Biol. Sci.* **265**(1413), 2373–2379.

Lyons, P. (2012). *The evolution of mutualism between alpheid shrimp and gobiid fishes: a balance between benefits and costs*. Doctoral dissertation, The Graduate School, Stony Brook University, Stony Brook, NY.

Lyons, P. (2013). The benefit of obligate versus facultative strategies in a shrimp–goby mutualism. *Behav. Ecol. Sociobiol.* **67**(5), 737–745.

McGraw, K.O. & Wong, S.P. (1996). Forming inferences about some intraclass correlation coefficients. *Psychol. Methods* **1**(1), 30.

McNamara, J.M., Barta, Z., Fromhage, L. & Houston, A.I. (2008). The coevolution of choosiness and cooperation. *Nature* **451**(7175), 189–192.

McNamara, J.M., Stephens, P.A., Dall, S.R.X. & Houston, A.I. (2009). Evolution of trust and trustworthiness: social awareness favours personality differences. *Proc. R. Soc. Biol. Sci. Series B.* **276**(1657), 605–613.

Michelangeli, M., Wong, B.B. & Chapple, D.G. (2016). It's a trap: sampling bias due to animal personality is not always inevitable. *Behav. Ecol.* **27**, 62–67.

Nelson, R.P. (2005). *A behavioral study of the Hawaiin goby shrimp relationship and the effects of predation on the system*. M.Sc Thesis, University of Hawaii.

Nussey, D., Wilson, A. & Brommer, J. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* **20**(3), 831–844.

Pellmyr, O., Leebens-Mack, J. & Huth, C.J. (1996). Non-mutualistic yucca moths and their evolutionary consequences. *Nature* **380**(6570), 155.

Schwagmeyer, P.L. (2014). Partner switching can favour cooperation in a biological market. *J. Evol. Biol.* **27**(9), 1765–1774.

Shrout, P.E. & Fleiss, J.L. (1979). Intraclass correlations: uses in assessing rater reliability. *Psychol. Bull.* **86**, 420.

Sih, A. & Bell, A.M. (2008). Insights for behavioral ecology from behavioral syndromes. In *Advances in the Study of Behavior*. Vol. **38**: 227–281. Brockmann, H.J., Roper, T.J., Naguib, M., WynneEdwards, K.E., Barnard, C. & Mitani, J.C. (Eds). San Diego: Elsevier Academic Press Inc.

Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004). Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **79**, 241–277.

Thacker, C.E. & Roje, D.M. (2011). Phylogeny of Gobiidae and identification of gobiid lineages. *Syst. Biodivers.* **9**(4), 329–347.

Thacker, C.E., Thompson, A.R. & Roje, D.M. (2011). Phylogeny and evolution of Indo-Pacific shrimp-associated gobies (Gobiiformes: Gobiidae). *Mol. Phylogenet. Evol.* **59**(1), 168–176.

Thompson, A.R. (2003) *Population Ecology of Marine Mutualists*. Ph.D. dissertation, University of California, Santa Barbara.

Thompson, A.R. (2004). Habitat and mutualism affect the distribution and abundance of a shrimp-associated goby. *Mar. Freshw. Res.* **55**(1), 105–113.

Thompson, A.R. (2005). Dynamics of demographically open mutualists: immigration, intraspecific competition, and predation impact goby populations. *Oecol.* **143**(1), 61–69.

Valerio, M., Mann, O. & Shashar, N. (2019). Boo! Did we scare you?: behavioral responses of reef-associated fish, prawn gobies (Amblyeleotris steinitzi and Amblyeleotris sungami) to anthropogenic diver disturbance. *Mar. Biol.* **166**(1), 1.

Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.

Wilson, A.D., Krause, J., Herbert-Read, J.E. & Ward, A.J. (2014). The personality behind cheating: behavioural types and the feeding ecology of cleaner fish. *Ethology* **120**, 904–912.

Wolf, M. & McNamara, J.M. (2012). On the evolution of personalities via frequency-dependent selection. *Am. Nat.* **179**(6), 679–692.

Wolf, M. & Weissing, F.J. (2012). Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* **27**, 452–461.

Wolf, M., van Doorn, G.S. & Weissing, F.J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proc. Natl Acad. Sci. USA* **105**, 15825–15830.

Yu, D.W. & Pierce, N.E. (1998). A castration parasite of an ant–plant mutualism. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 375–382.