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Published in: Biology Letters

DOI: 10.1098/rsbl.2021.0655

Published: 31/03/2022

Document Version Peer reviewed version

Link to publication on the UWS Academic Portal

Citation for published version (APA): Alexander, M. E., Skein, L., & Robinson, T. B. (2022). Rapid learning in a native predator shifts diet preferences towards invasive prey. *Biology Letters*, *18*(3), [20210655]. https://doi.org/10.1098/rsbl.2021.0655

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1	Rapid learning in a native predator shifts diet preferences towards invasive prey
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32 Abstract

Biological invasions often exert negative impacts on native communities and can disrupt a range of biotic interactions such as those between predators and prey. For example, when invasive species alter the foraging landscape, native predators can fail to recognise them as profitable prey because of unfamiliarity. This study therefore investigated whether a native predator (rock lobster Jasus lalandii) can develop a new preference for an invasive prey (mussel Semimytilus patagonicus) following conditioning through a short-term exposure. Conditioned lobsters, exposed to only S. patagonicus for a month, demonstrated a significant change in preference for the novel invasive prey, which was found to contrast with non-conditioned lobsters that continued to show predator preferences toward a native mussel (Choromytilus meridionalis). There is therefore potential for native predators such as J. lalandii to adapt and switch towards feeding on an abundant invasive prey, even if they avoid it at first. This indicates that rapid learning can occur in a species exposed to novel food resources and demonstrates that native species can adapt to biological invasions.

50 Keywords

52 Rapid learning, biological invasions, invertebrate predator, prey choice

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63 Introduction

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Invasions by non-native species can exert negative impacts on a range of biotic 65 interactions [1], including disruption to predator-prey relationships [2]. However, whilst 66 the effects of non-native predators on native prey communities have been well 67 68 documented (e.g. [3-5]), the impacts of non-native prey on native predators are comparatively understudied. Invasive prey species may displace competitively inferior 69 native prey, subsequently altering the native predator prey-base [6]. This can in turn 70 71 present native predators with several challenges, including the physical handling of 72 morphologically unusual prey [7] or overcoming toxic defence mechanisms of some 73 non-native species [8].

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The ability of a predator to switch from familiar to novel prey is important in the context 75 of efficient resource utilisation [9,10], and 'conditioning' (i.e. continuous exposure) 76 77 towards new prey is a mechanism through which this can occur. Such adaptive learning 78 is thought to occur more frequently in generalist predators compared to specialists, which often have fine-tuned adaptations to handle fewer, more specific prey types [11]. 79 80 Various factors have been proposed to influence conditioning, including past feeding experience [12,13], frequency of prey encounters [14] and predator handling capabilities 81 82 [11]. This concept of learning by native predators has often been investigated in relation to novel *toxic* prey [15–17], however as an adaptive response to invasions by *non-toxic* 83 84 prey, it has received less research attention.

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86 In South Africa, the west coast rock lobster Jasus lalandii is an important subtidal 87 generalist predator with a preference for mussel prey [18,19]. However, the mussel prey-base for this species is beginning to change due to the invasion by Semimytilus 88 patagonicus (formerly S. algosus), which is beginning to form a significant part of the 89 90 subtidal mussel community that comprised the native species Choromytilus meridionalis 91 and Aulacomya atra [20]. Previous work conducted in this region has shown that J. lalandii avoids S. patagonicus, preferring to select native C. meridionalis [21]. In 92 93 comparison to native mussels, the invasive species offers the greatest energetic reward

and has the weakest shells, making it a profitable prey choice for most mussel
predators [21]. Therefore, it is suggested avoidance occurs because of unfamiliarity with
the novel species, which many south coast rock lobster populations have yet to
encounter.

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99 The aim of this research was thus to determine whether the avoidance of *S*. 100 *patagonicus* by the rock lobster *J. lalandii* can be overcome through continuous 101 exposure (i.e. conditioning) to this invasive prey. As *J. lalandii* is a predator with a 102 flexible diet and invasive *S. patagonicus* is currently the most profitable mussel prey, it 103 was predicted that rock lobsters would switch from feeding on less profitable native 104 mussels to *S. patagonicus* once they become familiar with this species.

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107 Methods

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Mussels (*C. meridonalis, A. atra* and *S. patagonicus*) and rock lobsters *J. lalandii* of a standardised length were collected from the wild to be used in predation trials (see electronic supplementary information for details on collection sites and sizes of animals used).

- 113
- 114
- 115 Phase 1: Predator conditioning
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117 During a conditioning period, individual rock lobsters (n=20) were exposed to S. *patagonicus* prey only. This was conducted in individual cages (0.045 m³ in volume) 118 119 situated in the field (see electronic supplementary information) to ensure that rock 120 lobsters were exposed to S. patagonicus in the presence of naturally occurring cues. An 121 initial seven-day starvation period was conducted to allow for acclimatisation and to 122 standardise rock lobster hunger level. This was followed by four weeks of conditioning 123 where J. lalandii were fed with S. patagonicus in crushed and whole forms. The total 124 number of mussels (n = 40) provided to each lobster per week was kept constant throughout conditioning. The ratio of crushed to whole mussels was however
progressively adjusted as rock lobsters became more familiar with this prey species,
with only whole mussels offered in the final week (electronic supplementary information,
Table S1).

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131 Phase 2: Determining the influence of conditioning on prey preference

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To determine whether conditioning induced a switch in preference from *C. meridionalis* 133 134 to S. patagonicus, mussel selection from conditioned lobsters (Phase 1) was compared to that of non-conditioned individuals from the same population. The prey preference of 135 136 conditioned and non-conditioned J. lalandii (n=20 per treatment) took place in the laboratory (see electronic supplementary information). Feeding trials lasted seven days 137 138 after a seven-day acclimatisation and starvation period. Rock lobsters were provided 139 with one of two diet treatments which was either a 'current diet' or 'future diet' (n=10 per 140 diet for conditioned and non-conditioned lobsters). Diets comprised different proportions 141 of the three subtidal mussel species of interest reflecting their current and projected 142 occurrence in the field (Table 1; [20]). Mussel consumption was tracked daily, and 143 availability was kept constant throughout the trials.

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146 Statistical analyses

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All statistical analyses were conducted in R version 3.1.1 (R Core Team, 2016). The difference in overall prey consumption between non-conditioned and conditioned lobsters was analysed using a generalised linear model (GLM) with a quasi-Poisson error distribution and log link. Chesson selectivity indices [22] were calculated for each prey species (native *C. meridionalis* and *A. atra* and invasive *S. patagonicus*) through the formula:

155
$$\alpha_i = \frac{(r_i/p_i)}{\Sigma(r_j/p_j)}; j = 1, ..., n$$

where r_i/r_j is the proportion of a particular species in the diet (consumed), p_i/p_j the proportion of that species present in the overall habitat (on offer) and n the total number of prey species in the overall habitat (on offer). When $\alpha = 1/n$ neutral selection/the absence of selective predation in rock lobsters is indicated, whereas $\alpha < 1/n$ infers negative selection (avoidance) and $\alpha > 1/n$ positive selection (preference). This selectivity index is appropriate in this case as it accounts for the presence and proportion(s) of multiple species in the feeding landscape.

163 Chesson selectivity indices for different mussel prey species in each diet treatment for 164 both conditioned and non-conditioned lobsters were first arscine transformed due to 165 their proportional nature and then assessed using Friedman's ANOVAs. This was 166 followed by Conover post hoc tests to detect differences between Chesson selectivity 167 indices of prey species within each diet treatment. To establish whether conditioning 168 altered selection of a particular prey species, the Chesson selectivity indices of each 169 prey species as selected by conditioned and non-conditioned lobsters in each diet 170 treatment were compared using t-tests with a Bonferroni correction to account for 171 multiple comparisons.

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176 There was no statistical difference in the overall consumption of prey between nonconditioned and conditioned lobsters (GLM: $F_{1,27} = 0.411$, p = 0.53). There was however 177 178 a significant difference in the selection of mussel species by non-conditioned J. lalandii in both diet treatments (current diet: χ^2_2 = 7.153, p = 0.027, Fig. 1a; future diet: χ^2_2 = 179 180 7.517, p = 0.023, Fig. 1b). Here, lobsters showed a positive selection towards the native 181 mussel C. meridionalis regardless of the proportions in which it was present in the 182 overall diet. However, this selection was not found to statistically differ from the novel 183 prey, S. patagonicus, in the current diet (Fig. 1a). Prey selection by conditioned J.

Ialandii also differed significantly in both diet treatments (current diet: $\chi^2_2 = 6.869$, p = 0.032, Fig. 1c; future diet: $\chi^2_2 = 9.867$, p = 0.007, Fig. 1d), and conditioning of *J. Ialandii* to *S. patagonicus* drove significantly greater selectivity for the invasive species compared to native prey. This selection was evident regardless of the proportions in which prey were offered to *J. Ialandii*.

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190 Chesson selectivity indices for invasive S. patagonicus were significantly greater in 191 conditioned lobsters fed on both the current ($t_{11} = 2.402$, p = 0.035; Fig. 2a) and future diets ($t_{14} = 4.084$, p = 0.001; Fig. 2b). This was accompanied by a decreased preference 192 193 for the native C. meridionalis, as reflected by the lower selection for this species in 194 conditioned lobsters in both the current ($t_{11} = 3.115$, p = 0.009; Fig. 2a) and future diets 195 $(t_{14} = 2.656, p = 0.019; Fig. 2b)$. Finally, the selection index for native A. atra remained 196 low regardless of predator conditioning and regardless of diet treatment (current diet: t11 197 = 0.706, p = 0.495, Fig. 2a; future diet: $t_{14} = 0.221$, p = 0.828, Fig. 2b).

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200 Discussion

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The ability of predators to adapt to an altered prey base as a result of biological 202 203 invasions is important for ensuring that they will be able to incorporate such prey should 204 native resources decline or become fully displaced [7,23,24]. Therefore native predator 205 species that are able to do this may be more successful in the face of invasion fronts 206 that move through habitats, displacing native species rapidly [10]. This is likely to be 207 especially true of predators that can learn to adopt to consume new prey across short timescales. As such, we demonstrate in this study that, despite initial avoidance, a 208 209 native predator, the rock lobster J. lalandii, can come to preferentially select an invasive 210 mussel S. patagonicus through a period of rapid learning.

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After a short conditioning phase of four weeks, rock lobsters changed their diet preferences, as measured using Chesson selectivity indices [22], from the dominant native mussel *C. meridonalis* to the recent invader *S. patagonicus*. What was 215 noteworthy was that this occurred irrespective of the proportions of each prey species 216 appearing in the diet, with 'current' diets containing a greater number of native mussels 217 whilst 'future' diets contained more invasive mussels. The invasion of S. patagonicus on 218 the west coast of South Africa was first detected in 2009 [25], having recently been 219 found to have spread to the south coast [20]. Whilst this species represents a 220 morphologically similar prey to the native prey base, previous work reported that J. 221 lalandii avoided it for reasons that are not clear [21]. Native predators, however, could 222 be expected to shift towards feeding on a novel prey when there are low associated 223 search- and handling times, and when it offers higher energetic rewards compared to 224 other prey, as predicted by classic foraging theory [26]. It is also noteworthy that no preference was observed in any of the treatment combinations towards the native 225 226 mussel A. atra. Of the mussels on offer in this study, this species has the greatest shell strength and adductor muscle weight with an intermediate energy content [21] and was 227 228 therefore likely not selected due to a trade-off between these measures.

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230 The invasive mussel S. patagonicus is a more profitable prey, offering the greatest energetic reward with the weakest shells [21], and it is therefore possible that the native 231 232 predator is unfamiliar with other aspects of its presence such as its chemical signature. It is therefore likely that over the conditioning period, J. lalandii identified cues from 233 234 novel S. patagonicus and through continuous exposure learned to associate it with a 235 profitable food choice, leading to preference development. This ultimately drove rock 236 lobsters to seek out S. patagonicus, despite the presence and relative abundances of co-occurring native C. meridionalis and A. atra in the experimental arenas. Here, a 237 238 preference for S. patagonicus developed following exclusive exposure to this species for four weeks, however in a natural setting containing more prey species, the 239 240 development of this preference may be delayed. It is also unknown whether this 241 preference would persist over longer time periods or whether J. lalandii can retain a 242 memory for this new species. However, the strong feeding switch to S. patagonicus 243 observed in this study suggests that it might still be possible for rock lobsters to develop a preference for it in a setting where they will often encounter this species, which is 244

likely given the invasion history of *S. patagonicus* to date where it rapidly forms densebeds that exclude competitors [27,28].

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248 Conditioning through continuous exposure can lead to the development of a chemical 249 'search image' for a specific prey, which can subsequently improve the ability to locate 250 and ingest that prey [29]. Such chemoreceptive plasticity has been shown to be 251 important in animals that are omnivorous, long-lived, and found in various habitat types, 252 all of which can lead to variation in prey availability [30]. Thus, even though rock 253 lobsters are known to be generalist predators, variability in prey preference at an 254 individual level can be extreme. In addition, it has been suggested that rock lobsters may have a genetic predisposition to act on chemical cues from prey that are profitable 255 256 [31]. The ability to develop a chemical 'search image' for a particular prey (promoted through continuous exposure) can in itself be viewed as a mechanism that enhances 257 258 the detection and intake of profitable prey and is likely important here with the new 259 preference towards invasive, novel prey.

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359 Acknowledgements

360

Katie Keanly and Nicole Martin are thanked for help in collecting mussels. Andrea Plos is thanked for collecting rock lobsters and for the supply of rock lobster cages for the field component. We are also grateful to False Bay Yacht Club for providing space to maintain rock lobsters in the field.

- 365
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- 367 Funding
- 368

This work was supported by a Ph.D. fellowship award to Dr Lisa Skein from the DSI-NRF Centre of Excellence for Invasion Biology.

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373 Figure legends

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375 Figure 1. Median (interquartile range, minimum and maximum) Chesson selectivity indices for three prey species (Choromytilus meridionalis, Aulacomya atra and 376 Semimytilus patagonicus) as predated upon by non-conditioned rock lobsters in (a) 377 378 current and (b) future diet treatments, and conditioned rock lobsters in (c) current and (d) future diet treatments. Dots represent outliers. Boxes with different letters differ 379 380 significantly (Conover post hoc with Bonferroni correction). Values above the dashed line = positive selection (preference), on the line = neutral selection, below the line = 381 382 negative selection (avoidance).

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Figure 2. Species-specific comparisons between Chesson selectivity index values (mean \pm 1 standard error) for prey (*Choromytilus meridionalis*, *Aulacomya atra* and *Semimytilus patagonicus*) as predated upon by non-conditioned and conditioned *Jasus lalandii* in the (a) current and (b) future diet treatments. Values above the dashed line = positive selection (preference), values on the line = neutral selection and values below the line = negative selection (avoidance).

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400 Figure 1.



Table 1. Proportions of native C. meridionalis and A. atra, and invasive S. patagonicus that were presented to rock lobsters in current and future diet scenarios.

		Scenario	C. meridionalis	A. atra	S. patagonicus	
		Current	1	2	1	
		Future	1	1	2	
416						
417						
418	Rapid learning in a native predator shifts diet preferences towards invasive prey					
419	Alexander ME, Skein L, Robinson TB					
420						
421	Electronic Supplementary Information					
422						
423						
424	Specimen collection					
425						
426	This study was conducted in 2018 in the Western Cape, South Africa. Mussels were					
427	collected from monospecific beds at Bloubergstrand (33°48'01"S, 18°27'42"E) and					
428	Muizenberg (34°5'23"S, 18°29'45"E) with shell lengths of 20 – 30 mm. Rock lobsters (70					
429	- 100 mm carapace length) were collected from Kalk Bay on the south coast. This site					
430	was chosen as, by the time of our experiments, Semimytilus patagonicus had only					
431	recently spread to the south coast (2015) and was not known from the collection site.					
432	Thus, rock lobsters Jasus lalandii in this region would have had little to no exposure to					
433	this	species. Experi	imental trials took pla	ice during winter whe	en SST in northern False	
434	Bay	ranges betwee	en 14 - 15 °C (Dufe	ois & Rouault, 2012). Salinities are typically	
435	betv	veen 33 - 36 ppt	. Laboratory condition	ns had similar tempera	ature and salinity ranges.	
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438	Pha	se 1: Predator c	conditioning			
439						

440 The first phase of predator conditioning took place at False Bay Yacht Club, Simon's 441 Town (34°11'37"S, 18°26'08"E). Twenty lobsters were kept in separate cages (0.045 442 m³). These cages were covered with plastic mesh (0.5 x 0.5 cm) to exclude other 443 potential prey organisms from entering the cages. After a seven-day acclimatization 444 period, J. lalandii was fed with S. patagonicus in crushed and whole forms. The total 445 number of mussels given to each lobster per week was kept constant throughout the 446 conditioning phase (n = 40) and were added to each cage on the same day each week, 447 and not supplemented daily. Mussels were added via snorkelling to prevent the cages from being removed from the water to minimise disturbance to lobsters. As minimising 448 449 disturbance was a priority during this time, we were unable to quantify the exact number 450 of uneaten mussels. However, observations through the mesh cage indicated that 451 lobster feeding was saturated during this time with ~30 mussels consumed each week. It was suspected that avoidance of S. patagonicus already documented in non-452 453 conditioned lobsters may have been driven by unfamiliarity based on a different shell 454 morphology/chemical cue. Thus, crushed mussels were used to introduce lobsters to 455 the cues of this species and "teach" them to associate these cues with that particular shell shape over time. The ratio of crushed to whole mussels was then progressively 456 457 adjusted, with only whole mussels offered in the final week (Table S1).

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Table S1. Ratios of *S. patagonicus* in crushed and whole forms as adjusted over the predator conditioning phase.

Week	Crushed : Whole
1	30 : 10
2	20 : 20
3	10 : 30
4	0:40

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464 Phase 2: Determining the influence of conditioning on prey preference

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466 The prey preference of conditioned and non-conditioned J. lalandii took place in the 467 laboratory where single rock lobsters were kept in 38 L tanks in aerated seawater with 468 daily water changes. It should be noted here that non-conditioned lobsters were caught 469 from the field before being moved immediately into their acclimatization period in the lab 470 before feeding trials. Strict permit requirements along with a high poaching incidence in 471 the area resulted in the decision that it was too much of an experimental risk to have all 472 lobsters (conditioned plus non-conditioned) required in these trials suspended in cages 473 at the yacht club. Non-conditioned lobsters therefore remained in the wild for a month 474 prior to the trials, experiencing the same background water conditions as the nearby 475 yacht club whilst at the same time having access to a full natural diet.

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477 After the seven-day acclimatization period, rock lobsters were given either one of two 478 treatments: a 'current diet' or a 'future diet', each containing different proportions of the 479 three subtidal mussel species (native Choromytilus meridionalis and A. atra, and 480 invasive S. patagonicus) that occur in the region where rock lobsters were collected. 481 Proportions of mussel species in the 'current diet' was based on the latest assessment 482 of subtidal mussel populations in this region (Skein et al. 2018). Daily checks of 483 experimental tanks included the identification, removal and replacement of consumed 484 mussels so that proportions of different prey species were kept constant throughout the 485 experiments.

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487 Statistical analyses

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During feeding trials, some rock lobsters moulted or did not feed at all, an indication that they were soon to moult (Mayfield et al. 2000). These individuals were therefore excluded from statistical analyses. Consequently, although trials began with 10 replicates for each diet treatment in conditioned and non-conditioned lobsters, analyses of conditioned lobsters included six replicates for the 'current diet' treatment and eight
for the 'future diet' treatment, while for non-conditioned lobsters there were seven
replicates of the 'current diet' and eight for the 'future diet'.

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