Eat and be eaten: reciprocal predation between axolotls (Ambystoma mexicanum) and crayfish (Cambarellus montezumae) as they grow in size

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Eat and be eaten: reciprocal predation between axolotls (*Ambystoma mexicanum*) and crayfish (*Cambarellus montezumae*) as they grow in size

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Information about predator–prey relationships in aquatic systems can be helpful to improve the conservation management of endangered species. Restoration efforts for the endangered axolotl (*Ambystoma mexicanum*) involve the creation of refuges to increase the occurrence of suitable conditions for native species. Little is known about the predator–prey interaction between the axolotl and the native crayfish (*Cambarellus montezumae*) that also inhabits the refuges. To understand this interaction, we designed a set of experimental arenas and investigated both species at various life stages. Our findings suggest a switch in the predator–prey relationship between crayfish and axolotls at lengths between 2.6 and 3.5 cm. Individuals of both species below this size-range serve as prey, whereas larger individuals become predators. The 66.7% of crayfish that were preyed upon by axolotls were of intermediate size, whereas adult crayfish primarily consumed newly hatched axolotls (70%). We discuss the implications of this native species interaction with respect to their habitat conservation.

Keywords: Xochimilco; crayfish; restoration; feeding; salamander

Introduction

Predator–prey interactions have proven to be a key factor in aquatic ecosystem dynamics (Scheffer 1998). These interactions modulate the population dynamics of the species that shape the structure of the aquatic community (Mittelbach & Chesson 1987). Predator–prey interactions must therefore be understood to support the implementation of conservation or restoration programs *in situ* for endangered species (Vander Zanden et al. 2006; Engeman et al. 2009).

A good example of this principle is furnished by the efforts for the conservation of axolotls (*Ambystoma mexicanum*) in their native wetland. Wild populations of axolotls have been alarmingly reduced, from 6000 to 100 per km^2, between 1998 and 2007 (Graue 1998; Zambrano et al. 2007). This amphibian is endemic to the Valley of Mexico, and the only remaining populations of the species occur in the Xochimilco wetland system in Mexico City. The axolotl is consequently under special protection according to the Mexican Official Regulation (NOM-059-SEMARNAT 2010), in CITES Appendix II (CITES 2012) and is listed with a status of critically endangered in the

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IUCN Red List (IUCN 2012). Decreases in populations of this salamander are related to variables such as water quality (Contreras et al. 2009), urbanisation processes (Merlín-Uribe et al. 2013) and the overabundance of exotic fish species (Zambrano et al. 2010a). The distribution of axolotls within the wetland has been reduced as a result of small patches within the native range in Xochimilco (Contreras et al. 2009).

Efforts at axolotl restoration involve the creation of refuges (Valiente et al. 2010), which are canals surrounding islands where traditional agriculture (*chinampas*) is practiced without the use of chemicals or any type of infrastructure (Von Bertrab & Zambrano 2010). In the axolotl refuges, the water quality is improved by the action of native aquatic macrophyte filters and the exclusion of exotic fish species. Axolotls (*A. mexicanum*) and other native species such as the silverfish (*Menidia jordanni*) and the crayfish (*Cambarellus montezumae*) are able to survive in these refuges (Valiente et al. 2010).

Although the refuges have been successful (Valiente et al. 2010), little is known about the predator–prey interactions of the axolotls, particularly with native species. These interactions may be intense because refuges are small (1.80×20 m) and these species may coexist in a limited area compared with the total wetland that represents their former range (Valiente et al. 2010). Predator–prey interactions with native species in these small areas may change the population dynamics of the axolotl (McCauley et al. 1993; Claessen et al. 2002) even in a system with water quality suitable for axolotls and with sufficient other resources such as food and space.

Axolotls and crayfish share the same habitat in the Xochimilco wetlands. Both species inhabit the benthic zone, and female axolotls lay their eggs on sheltering macrophytes such as the hyacinth (*Eichhornia crassipes*) and elodea (*Egeria densa*) (Marín 2007), the same plants used by crayfish as refuge and recruitment sites (Hobbs 1993; Rangel 2004). This increases the probability that the two species will interact. These interactions can be complex because both species change their food sources ontogenetically. This factor may be particularly critical for the survival of the axolotl because a population matrix analysis suggests that its population growth rate is highly sensitive to small changes in the survival rate of eggs and the juvenile stages (Zambrano et al. 2007).

Adult axolotls occupy one of the top positions in the food web (Zambrano et al. 2010b). They are passive predators that normally take prey found near their mouths (Zambrano et al. 2011). Juvenile axolotls are more active and feed upon microinvertebrates such as zooplankton and nematodes (Smith & Petranka 1987; Bardwell et al. 2007), whereas adult axolotls eat small fish, crayfish, annelids and insects, although plants and filamentous algae have been found in the gut contents of wild caught animals (Zambrano et al. 2010a). In contrast, little is known about the ecology of Xochimilco crayfish. The crayfish capture small vertebrates and insects and forage with their chelae for food items hidden in the sediment (Rangel 2004; Zambrano et al. 2010a).

The ability of a predator to ingest a prey item depends on both size and biomass, including the size and biomass of the predator itself (Cohen et al. 1993). This relationship is based on morphological limitations, such as the predator's mouth size (Persson et al. 1996); and on other attributes derived from size, such as mobility; or other characteristics of prey defence (McCauley et al. 1993; Christensen 1996). Prey larger than the width of an axolotl's throat, for example, is rapidly rejected because the amphibian can die by choking on large prey items (pers. obs.). Similarly, prey larger than the crayfish chelae can escape easily and the capture efficiency for this prey is low (pers. obs.).

The aim of our study was to understand the predator–prey interactions between axolotls and crayfish. Predator–prey relationships involving animals of different sizes can

be used to evaluate interactions between them that influence the population growth rates of both species. This information can be crucial for determining the effects of species loss on ecosystem stability (McCann 2000; Loreau et al. 2001) and the potential restoration of the species through the creation of refuges (Valiente et al. 2010) in which the species coexist.

Materials and methods

Eggs, juveniles and adult axolotls were obtained from the experimental facilities at the Laboratory of Ecological Restoration (Biology Institute, National Autonomous University of Mexico (permit FAUT:0112). All of the amphibians used in these experiments were therefore born in captivity. Crayfish were collected in the field by capturing them from canal banks with a 1.5 m wide triangle net. They were then transported to the laboratory in 7 l plastic containers filled with water from the lake. Ovigerous female crayfish were isolated to increase their offspring survival rate.

Two weeks before the start of the experiments, the organisms from both species were selected and removed based on size classes to avoid cannibalism. All of them were kept in separate experimental containers with constant conditions of water, temperature and food quantity. Crayfish were fed with commercial pellets for aquarium fish. The adult and juvenile food for axolotls was based on small living fish in the same way as they are normally fed in the laboratory. They therefore hunted for their food in both cases. We provided *Artemia salina*, *Daphnia sp* and *Tubifex sp* for larval axolotls. Food was provided *ad libitum* in all cases.

Five treatments were established for testing without replacement of the original organisms: (1) One adult axolotl (mean 24.3 ± 2.65 cm) vs. five crayfish (10 repetitions). For this treatment, crayfish were categorised according to their sizes in five intervals: (a) newly hatched (0.5 cm); (b) organisms between 0.6 and 1.5 cm; (c) organisms between 1.6 and 2.5 cm; (d) organisms between 2.6 and 3.5 cm; and (e) organisms larger than 3.5 cm, with a maximum of 4.5 cm. Each size interval of crayfish was represented in every repetition by one individual. (2) One juvenile axolotl (3.35 ± 0.95 cm) vs. five newly hatched crayfish (mean of 0.5 cm, 15 repetitions). (3) One adult crayfish (3.49 ± 0.34 cm) vs. five juvenile axolotls. To avoid axolotl cannibalism, we generated three sub-treatments according to the size categories of the amphibians: (a) 1.0–1.5 cm (10 repetitions); (b) 1.6–2.5 cm (8 repetitions); and (c) 2.6–3.5 cm (8 repetitions). (4) One juvenile crayfish (2.51 ± 0.68 cm) vs. five newly hatched axolotls (1.0–1.5 cm) (11 repetitions). (5) One adult crayfish (3.46 ± 0.44 cm) vs. five axolotl eggs (10 repetitions).

All the containers were filled with tap water. Two drops of anti-chlorine per litre (Clorkill, Bioma Labs) were added. The treated water was oxygenated with air pumps for 15 min before the organisms were placed into the container. Treatments with predators smaller than 5.5 cm were performed in plastic arenas with a diameter of 20 cm, filled with 1.3 l of treated water. Treatments in which predators were larger than 21 cm were performed in 60 cm diameter fiberglass containers filled with 28.3 l of treated water. We kept the proportion between the predator length and the container diameter as close as possible to one-third to increase the number of encounters between predators and prey. Each container was visually isolated by placing an opaque white cover over the side of the container to reduce external disturbances.

Both types of containers were divided into two equal parts by a net. A predator was placed on one side and five prey randomly placed on the other side. The division of the

container was maintained for 15 h during which no food was supplied. The net was then removed for 8 h. The interaction was recorded with digital video cameras previously installed to record the number of attacks and the occurrence of prey consumption.

An axolotl attack was defined as an attempt to catch a crayfish by rapid opening and closing of the mouth in the direction of a prey item. Capture occurred when a crayfish was successfully taken and consumed after the attack. A crayfish attack was defined as a scissor movement performed by the crayfish with its chelae directed towards the axolotl. Capture was defined as the successful grasping and consumption of the axolotl.

The numbers of attacks and captures were counted to calculate predation efficiency (captures/attacks). The relationship between predator size and capture efficiency was analysed with a regression analysis, using each repetition as a single data point. We estimated the sizes that were most vulnerable to predation as well as the sizes at which the prey became predators.

Results

Adult axolotls preyed upon all sizes of crayfish. Most crayfish consumed as prey, however, belonged to two size intervals – 0.6–1.5 cm and 1.6–2.5 cm – representing 66.7% of the total captures (Figure 1). The largest prey captured did not exceed 17% of the size of the axolotl (Appendix 1).

Adult crayfish similarly captured all sizes of juvenile axolotls but showed a preference for newly hatched axolotls (1.0–1.5 cm) representing more than 70% of the total captures (Figure 2). Captures by adult crayfish decreased markedly when they were placed with larger axolotls. The fewest captures – in fact, only 3% of the total – occurred for the size interval containing the largest axolotls (2.6–3.5 cm, Figure 2). Juvenile crayfish fed on newly hatched axolotls with a 5% success rate. All crayfish consumed at least one egg in the treatment in which crayfish were placed with axolotl eggs (Appendix 1).
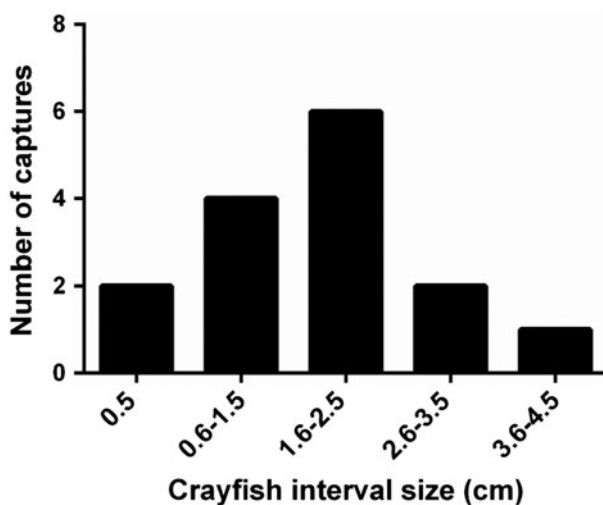
Figure 1. Number of captures by adult axolotls according to the prey size interval.
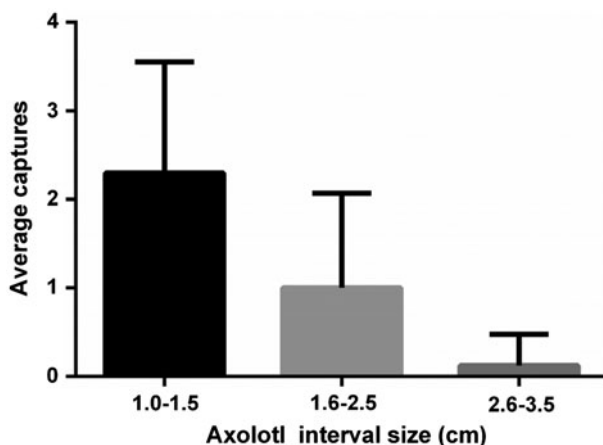
Figure 2. Average of captures by adult crayfish according to their prey sizes (lines represent standard deviation).
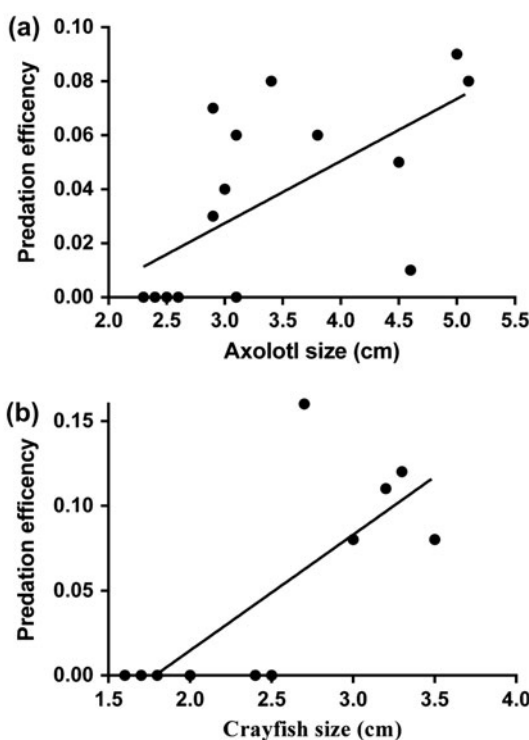
Figure 3. Relationship between size and predation efficiency for juveniles in: (a) axolotl and (b) crayfish.

A strong relationship between predation efficiency and axolotl size was observed in juvenile axolotls ($R^2 = 0.42$, $F = 9.93$, $p < 0.05$; Figure 3(a)). In contrast, no such relationship was found for adult axolotls ($R^2 = 0.25$, $F = 2.79$, $p = 0.13$). In juvenile
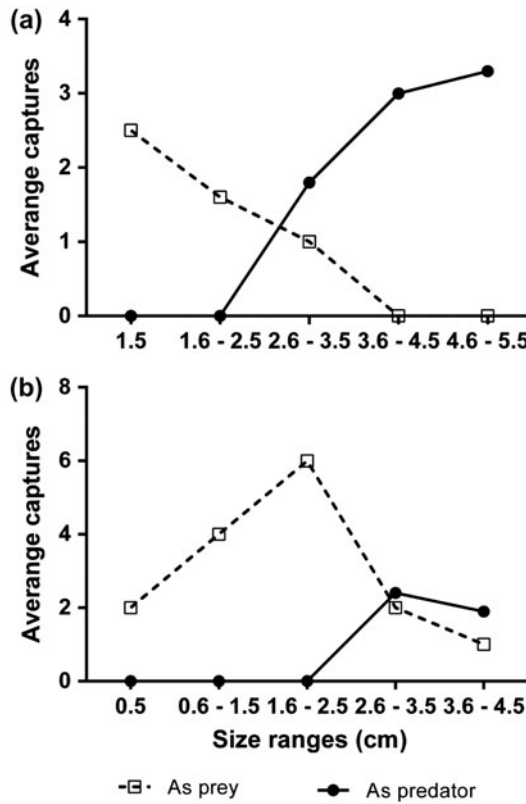
Figure 4. Size range at which role reversal occurs for each species: (a) axolotl and (b) crayfish.

crayfish, as in juvenile axolotls, a strong relationship was found between size and predation efficiency ($R^2 = 0.58$, $F = 12.21$, $p < 0.05$; Figure 3(b)). In contrast, no such relationship was found in adult crayfish in any of the subtreatments: a ($R^2 = 0.003$, $F = 0.03$, $p = 0.86$); b ($R^2 = 0.23$, $F = 1.81$, $p = 0.22$); or c ($R^2 = 0.07$, $F = 0.45$, $p = 0.52$; Appendix 1). No relationship was found between crayfish size and the number of eggs captured ($R^2 = 0.31$, $F = 3.62$, $p = 0.09$; Appendix 1).

Newly hatched axolotls measuring up to 2.6–3.5 cm were subject to predation by adult crayfish. When axolotls attained a size greater than 3.5 cm, they behaved as predators (Figure 4(a)). Similarly, crayfish less than 3.5 cm in size were more susceptible to predation than larger ones, which were more able to capture axolotls (Figure 4(b)).

Discussion

The fact that axolotls prey successfully on smaller crayfish suggests that larger crayfish are better able to escape predation, either because larger prey are more difficult to handle (Allan et al. 1987; Barbeau & Scheibling 1994; Hosseini et al. 2005) or because larger crayfish are more aggressive and the size of their chelae allows for more efficient predator defence (Stein & Magnuson 1976; Garvey & Stein 1993). The size relationship between predator and prey and the foraging techniques of the predator are factors that determine predator efficiency (Hughes & Dunkin 1984). Predation satiation is another

potential influence that may affect the capture efficiency. We did not, however, observe a predator behavioural change after they consumed their first prey (pers. obs.). All the predators chased and attacked their prey throughout the entire experiment with apparently the same intensity. Almost 24% of them predated upon more than one prey type and 1.5% consumed all types of prey that were offered. Considering the number of prey provided during the experiment and the exposure time, predation satiation may have played a minor role in predator efficiency.

Capture strategy is important for understanding how the axolotl selects its prey. Two strategies were observed in this study. First, in the passive strategy, the axolotl waits for a potential prey item to pass by its head. When that occurs, the axolotl quickly opens and closes its mouth towards the item. The wide mouth of the axolotl generates a suction effect, and this suction pulls the prey into the salamander's mouth in a fraction of a second. This strategy is commonly known as "gape and suck" (Özeti & Wake 1969). In the second predation strategy, the axolotl approaches the prey slowly with its mouth close to the bottom of the container. This active strategy was less effective because the prey escaped 90% of the time (pers. obs.). The axolotl only feeds on prey that is appropriate for the size of its mouth opening because it commonly uses the passive strategy to forage.

Crayfish also show active and passive predation strategies. The active strategy consists of approaching the prey slowly until it can be reached with the chelae. In the passive strategy, the crayfish waits motionlessly for the approach of the prey. Both strategies are highly efficient if the prey is a newly hatched axolotl (pers. obs.). Although crayfish also attack larger prey, the efficiency of predation on this prey decreases, as is the case with the predatory behaviour of other crustaceans (Mascaro et al. 2003). The difficulty of handling prey increases with prey size (Allan et al. 1987; Barbeau & Scheibling 1994; Hosseini et al. 2005).

Older organisms have been reported to possess better hunting skills (Hance & Van Impe 1999). Larger individuals should therefore show greater predation efficiency than smaller individuals. In this context, the juvenile stages of both species exhibit a strong relationship between size and predation efficiency, but this relationship is not present in adults. These findings could be due to the laboratory conditions which may have affected the predation skills (Rubbo et al. 2006). Further behavioural studies must therefore be undertaken to gain an understanding of these differences.

Early juvenile stages at sizes that are not sufficiently large to avoid predation are more susceptible to crayfish capture. Juvenile axolotls also begin to feed on newly hatched crayfish at these same stages. Small crayfish are subject to predation by axolotls. Crayfish of sizes greater than 3.5 cm are, however, more difficult prey because their defensive skills increase. When crayfish attain sizes greater than 3 cm, they can begin to prey on axolotl eggs and newly hatched young.

The size structure of a population can be modified by predator–prey interactions and can therefore be used to understand trophic web stability (Emmerson & Raffaelli 2004). Changes in the proportions of age classes in a population of predators place differential pressure on certain prey sizes (Cohen et al. 1993; Emmerson & Raffaelli 2004), with resulting effects on population dynamics (Claessen et al. 2002). Clearly, these interactions become more complex if predator–prey relationships involving more species are included (Cohen et al. 1993; Zambrano et al. 2010b).

This study contributes to the understanding of the predator–prey interactions between *A. mexicanum* and *C. montezumae*. Furthermore, this research provides evidence that adult crayfish can feed on eggs and newly hatched axolotls. This result explains the finding, based on isotopic signatures, that crayfish occupy a high position

on the food web map (Zambrano et al. 2010a). In addition, the early life stages are the most sensitive within their lifespan (Zambrano et al. 2007). This predator–prey relationship may consequently have a strong influence on this amphibian population. It is especially necessary, in this case, to understand the impact of predation–prey relationships within the refuges in the Xochimilco freshwater system.

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Appendix 1

Attacks and captures according to treatment. In treatment 1, the prey size is reported in intervals: (1) newly hatched (0.5 cm); (2) organisms between 0.6 and 1.5 cm; (3) organisms between 1.6 and 2.5 cm; (4) organisms between 2.6 and 3.5 cm; and (5) organisms larger than 3.5 cm (with a maximum of 4.5 cm).

Predator (cm)	Prey (cm)	Attacks (No)	Capture (No)	Efficiency (%)
Treatment 1: Adult axolotls vs. various crayfish interval sizes				
28	1,2,3,4,5.	3	1	0.33
27.5	1,2,3,4,5.	1	1	1
26	1,2,3,4,5.	5	0	0
26	1,2,3,4,5.	29	2	0.07
26	1,2,3,4,5.	8	1	0.13
23	1,2,3,4,5.	10	4	0.4
22	1,2,3,4,5.	1	0	0
22	1,2,3,4,5.	20	1	0.05
21.5	1,2,3,4,5.	36	2	0.06
21	1,2,3,4,5.	61	3	0.05
Treatment 2: Juvenile axolotls vs. newly hatched crayfish				
5.1	0.5	60	5	0.08
5	0.5	43	4	0.09
4.6	0.5	88	1	0.01
4.5	0.5	57	3	0.05
3.8	0.5	47	3	0.06
3.4	0.5	12	1	0.08
3.1	0.5	10	0	0
3.1	0.5	34	2	0.06
3	0.5	50	2	0.04
2.9	0.5	41	3	0.07
2.9	0.5	32	1	0.03
2.6	0.5	20	0	0
2.5	0.5	11	0	0
2.5	0.5	16	0	0
2.4	0.5	3	0	0
2.3	0.5	5	0	0
Treatment 3: Adult crayfish vs. juvenile axolotls				
4.2	1.0–1.5	19	2	0.11
4	1.0–1.5	28	1	0.04
4	1.0–1.5	18	5	0.28
4	1.0–1.5	36	1	0.03
3.8	1.0–1.5	78	1	0.01
3.6	1.0–1.5	37	2	0.05
3.5	1.0–1.5	37	3	0.08
3.3	1.0–1.5	25	3	0.12
3.2	1.0–1.5	28	3	0.11
3	1.0–1.5	25	2	0.08
3.4	1.6–2.5	38	3	0.08

Appendix 1. (*Continued*).

Predator (cm)	Prey (cm)	Attacks (No)	Capture (No)	Efficiency (%)
3.4	1.6–2.5	19	0	0
3.3	1.6–2.5	45	1	0.02
3.3	1.6–2.5	36	2	0.06
3.2	1.6–2.5	43	1	0.02
3.2	1.6–2.5	28	0	0
3.1	1.6–2.5	36	0	0
3.1	1.6–2.5	65	1	0.02
4.1	2.6–3.5	41	0	0
3.7	2.6–3.5	51	1	0.04
3.5	2.6–3.5	34	0	0
3.5	2.6–3.5	44	0	0
3.4	2.6–3.5	35	0	0
3.4	2.6–3.5	40	0	0
3.3	2.6–3.5	30	0	0
3.3	2.6–3.5	28	0	0
Treatment 4: Juvenile crayfish vs. newly hatched axolotls				
3.5	1.0–1.5	37	3	0.08
3.3	1.0–1.5	25	3	0.12
3.2	1.0–1.5	28	3	0.11
3	1.0–1.5	25	2	0.08
2.7	1.0–1.5	25	4	0.16
2.5	1.0–1.5	17	0	0
2.4	1.0–1.5	9	0	0
2	1.0–1.5	13	0	0
1.8	1.0–1.5	14	0	0
1.7	1.0–1.5	7	0	0
1.6	1.0–1.5	10	0	0
Treatment 5: Adult crayfish vs. axolotl eggs				
(Only captures are shown, NA = not applicable)				
4.1	NA	NA	4	NA
4	NA	NA	2	NA
3.8	NA	NA	1	NA
3.7	NA	NA	2	NA
3.5	NA	NA	2	NA
3.4	NA	NA	1	NA
3.2	NA	NA	2	NA
3.1	NA	NA	1	NA
3	NA	NA	2	NA
2.8	NA	NA	1	NA