Department of Physics, Chemistry and Biology

Master Thesis

Reintroducing captive bred species – a community ecological perspective

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Sammanfattning
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1. Abstract

Throughout history species has gone extinct due to anthropogenic activities. During the last century efforts have been done to reintroduce species back into the wild. Zoos that originally were created as amusement parks for people have today a new purpose; to keep and breed species in captivity for later reintroductions in the wild. However a relaxed environment such as a zoo leads to a general fitness decline of up to 40% per generation in captivity. The probability of a successful reintroduction of a species that has been bred in a zoo will be lower the longer time it has been kept in captivity. The reintroduction of a captive bred species can also cause secondary extinctions and other negative effects on the food-web. Both changes in the community caused by the loss of a species and changes in the species itself caused by captivity can be expected to affect the outcome of a reintroduction attempt. Using a modeling approach I here investigate how the reintroduction of a captive bred species (at three different trophic levels; basal, intermediate and top predator species) affects a food-web and what risks there are in reintroducing it. A Lokta-Volterra model with type II functional response is used. I investigate three scenarios: the reintroduction of a species with 0% change in its attributes, 40% change in its attributes and 75% change in its attributes. It was found that the most important factor for reintroduction success when reintroducing a species is whether it is a producer species (basal species) or a consumer species (intermediate and top predator species). The producer species were most sensitive to the changes in their attributes, whilst consumer species were more sensitive to change in the food-web (Euclidian distance). The producer species were found to cause most secondary extinctions in all scenarios, hence indicating that it is a bottom-up controlled food-web. The present study suggests that the success of a reintroduction attempt is affected both by the degree of changes in the food web caused by the initial loss of the species and the degree of change in the species itself caused by captivity.

Keywords: Captive breeding, species reintroductions, species interactions, food-web, secondary extinctions, Lokta-Volterra models.

2. Introduction

Throughout history species has disappeared from their natural ranges due to anthropogenic activities. Although mankind has introduced species into the wild for more than a millennium, it is only in the last 100 years conservationists have reintroduced species to their historical natural habitat in an effort to “undo” the damages caused by mankind (Armstrong & Seddon, 2007, Frankham, 2010, Montoya et. al., 2006, Seddon et. al., 2006). Since 1990 there has been a growing interest in the field of species reintroductions, not only in the scientific world but also in the general public. This has caused zoos to take a more conservation-oriented approach in their work in order to try to prevent species extinctions in the wild (Seddon et. al., 2006).

When species are endangered and their habitats are being destroyed due to anthropogenic activities the only option is to capture some individuals or in the worst case scenario all individuals in a population of a species and take them into captivity. Today there is room for some 500 species in zoos around the globe, however it has been calculated that approximately 2000-3000 terrestrial vertebrate species alone is in need of captive breeding in the future (Frankham, 2008). The main goal for captive-breeding programs is to reinforce the population of a wild endangered species, however several studies have shown that the reintroductions of captive bred species have very low success-rates, between 10-40% chance of success (this depending on how “success” is defined in the studies) (Robert, 2009). The main reason for the low success-rate is the general deterioration that occurs when a species is put into a “relaxed” environment such as a zoo. This meaning that the natural selection that occurs in the wild is put aside since the survival-rate in zoos can be more than ten-fold higher than in the wild (Araki, 2007).

2.1. Effects of captivity on species

It is common to use captive bred animals for reintroductions; they can be used as a buffer if the natural population goes extinct in the wild. However there are certain drawbacks in using this technique, for instance problems with genetic deterioration, behavioral disorders or other changes in the attributes of captive bred species (Faria et al., 2010, Aaltonen et al., 2009, Robert, 2009, Williams & Hofman, 2009). According to Araki et al. (2007) the effects of captivity on species are in general a 40% decline in fitness per generation. The reasons for this are mainly due to genetic deterioration and behavioral disorders. The evolutionary aspects of captive breeding is brought up by Robert (2009), he concludes that the fecundity in captive bred populations is much higher than in wild ones. Hence natural selection is weakened and species might go through an evolutionary change, meaning that they cannot return to their initial natural range since they do not fit into the food-web anymore. This means that with every generation kept in captivity there is a smaller chance of a successful reintroduction. Thus, it would be preferable to have the endangered species in captivity as short time as possible. This is rarely the case, some species may have to spend 100-200 years in captivity before their natural habitat is restored, making it hard to successfully reintroduce the species (Frankham, 2008). The optimal time spent in captivity is 10-20 generations according to Robert (2009) and Theodorou & Couvet (2004). Their explanation for this being that there is a tradeoff between time spent in captivity and population size of the captive bred species. A short time in captivity means small population size and small changes in the species attributes while a long time means large population size and large effects on the species attributes.

Far from all species or subspecies are capable to live and thrive in captivity, for example two taxonomically close species can adapt very differently to captivity. This because some species might have higher “demands” than others or that the preconditions for a species to thrive in captivity is unknown. A tendency is that species rare in the wild is also harder to keep in zoos and these are the species most in need of captive breeding (Mason, 2010).

2.2. Changes in the food web structure caused by species loss

During the time a species spend in captivity it is not only its traits that change, the ecosystem in which it once lived may also undergo significant changes that can affect the reintroduction success. When a species goes extinct, the ecosystem does not just stay the way it was, and it can react differently depending on what place and function the extinct species had in the community (Naeem et. al. 1994). In worst case scenarios there is a risk for the whole ecosystem to collapse due to trophic cascade effects caused by the extinction of one species, whereas in other cases there are few secondary extinctions or none at all (Ebenman & Jonsson, 2005). Since empirical studies (for obvious reasons) are hard to conduct theoretical modeling is used to get a better understanding of how food-webs react to species loss and reintroductions (Christanou & Ebenman, 2006). There is a risk that the system has changed and “closed” itself from future reintroductions of species (Lundberg et al., 2000). For example, if there are two species competing with each other and one of them disappears from the ecosystem, then the other species takes over the niche and grows in population size, making it virtually impossible for the extinct species to return back into the food-web (Lundberg et. al., 2000). The strength of the interaction links between species is essential when it comes to how an ecosystem reacts to species extinction. The link-strength is not the only vital parameter of an ecosystem; also species richness and connectance are vital when it comes to the robustness of a food web to species loss (Ebenman et. al., 2004). For example, if there are few connections between species in a food web, the risk of secondary extinctions is much higher compared with food webs with many connections (Dunne & Williams, 2009, Eklöf & Ebenman, 2006). Christanou & Ebenman (2006) list four possible outcomes when a species is reintroduced into a food web (see fig. 1).

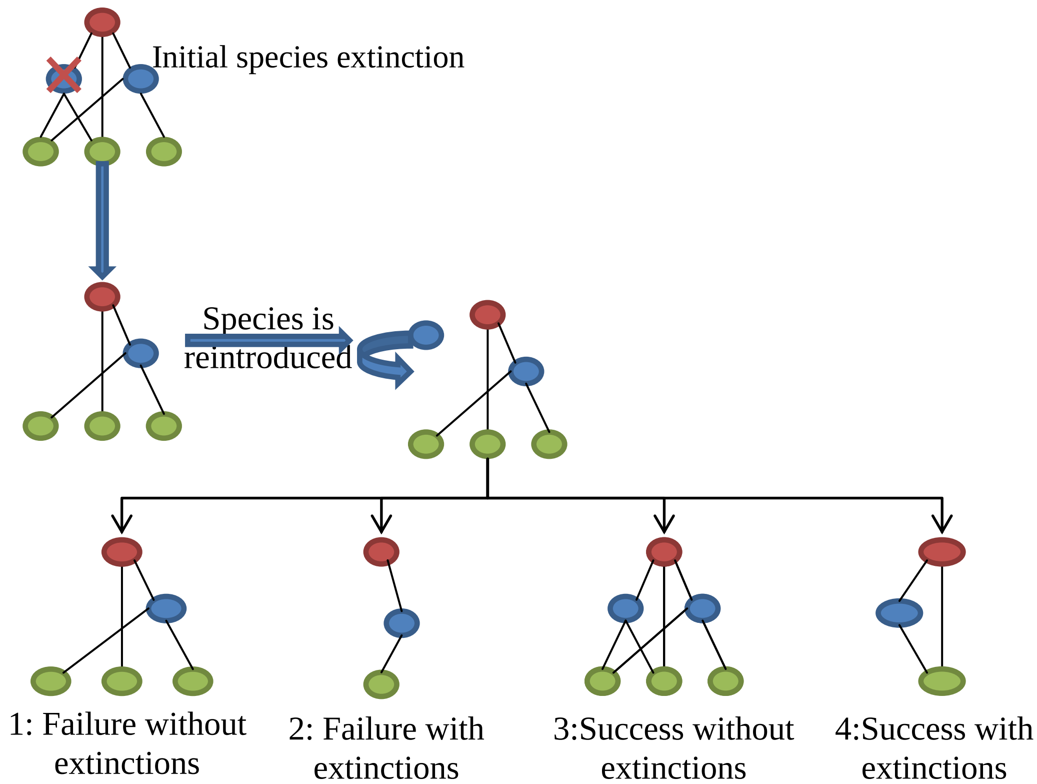

Fig 1. Four potential outcomes of a species reintroduction: I) The system or the species itself has changed too much for the reintroduced species to survive in the system, II) The reintroduced specie can survive for a while but cause secondary extinctions and in the end goes extinct itself, III) The system and the reintroduced species have not changed significantly from the initial deletion causing success without any secondary extinctions. IV) The reintroduced species is strong enough to survive and exclude other species in the food-web causing secondary extinctions (from Christanou & Ebenman 2006).

2.3. Effects of a reintroduction

Not only can the loss of a species affect the food-web, but also the reintroduction can cause damage and secondary extinctions, especially if there were secondary extinctions caused by the initial loss of the species (Fowler & Lindström 2002). Laikre et al. (2010, p. 520) lists four additional risks with reintroducing a captive bred species back into the wild: (I) loss of genetic variation, (II) loss of adaptations, (III) change of population composition and (IV) change of population structure. They further state that these risks are largely neglected today, especially in the commercial markets such as hunting, forestry or fishing industry where enormous numbers of animals are released and plants set out each year.

The effects on food-webs when a captive bred species is reintroduced have not yet been studied to any further extent. Since we know that the invasion of alien species can alter the whole structure of a food-web it is also important to see how the food-web reacts to a reintroduction of a species with changed attributes caused by captivity (Eklöf & Ebenman, 2006. Ebenman et al. 2004).

In this thesis the focus will be on how a food-web reacts to the extinction of a species and its later reintroduction to the food-web. All species in the system will be deleted and later reintroduced (one at a time) in order to estimate what impact their disappearance and reintroduction have on the food web. These species will have different attributes and functions in the system.

3. Methods

The method used in this thesis was mathematical modeling performed in the program Matlab. The analyses are based on Christianou & Ebenman's (2006) deterministic food-web models which they used for reintroducing species into communities. The model community that was generated is a triangular shaped food-web with 12 species divided into three trophic levels; five basal species (primary producers), four intermediate species (links both up and down in the food-web) and three top predator species (only links down in the food-web). Each species was removed from the food-web one at a time. When the species was removed from the ecosystem its attributes (mortality- or growth-rate, depending on if the species is a consumer or a producer) was changed with 40% and 75%, as if they were kept in captivity during their absence from the ecosystem. The mortality/growth-rate was used since it is a good measure of several changes (introduction, 2.3., p.7) in a captive bred species, for example, genetic depression, weakened predator skills and infertility all affect these rates. Different mortality-/growth-rates were used due to the fact that captivity alters the mortality of species in different extent and can also be illustrated as a shorter/ longer time spent in captivity (Aaltonen et. al., 2009). As a control the species was removed and reintroduced without any change in its mortality/growth-rates (0% change). When the species was removed and then reintroduced to the food-web, the effects of this was assessed and statistically analyzed.

3.1. The model

The model food-webs were generated using an existing model (Chrsitianou & Ebenman 2006). In order to model the dynamics of the model food-webs Lotka-Volterra equations were used:

$$\frac{dx_i}{dt} = x_i\left(b_i + \sum_{j=1}^{n} \alpha_{ij}\, x_j\right)$$

where dx_i/dt is the rate of change of density of species i over the time in a community with the number of species (n). The density of species i is described as x_i and b_i is its per capita growth rate (if species i is a basal species, if it is a consumer then b_i is the intrinsic mortality rate). The interaction between species i and j is given by α_{ij} which is the per capita effect that species j has on species i:s per capita growth rate.

Two types of functional responses were used; type I when constructing the food-web and type II when modeling the food-web:

$$(1) \propto_{ij}^{I} = h_{ij}\beta_{ij}$$

$$(2) \propto_{ij}^{II} = \frac{h_{ij}\beta_{ij}}{1+T\sum_{k\in R(j)} h_{kj}\beta_{kj}x_k}$$

Equation (2) shows the expression for α in the Lotka-Volterra equation with a type II functional response. The main difference between type I functional response (1) and type II functional response (2) is that in type II the per capita effect (α) of the predator on the prey is dependent on the population size of the prey species. β_{ij} is the intrinsic attack-rate on species *i* and h_{ij} is the preference of predator *j* for prey species *i*. *T* is the time it takes for a predator to handle (catch and consume) its prey.

3.2. Parameters

There are three trophic levels in the food-webs investigated here; basal, intermediate and top predator species. The basal species have a growth-rate (b_i) of 1 and if it is an intermediate species it will have a mortality-rate (b_i) of -0.01 and the top predator species have a mortality rate of -0.001. The reason for giving the top predator species a lower mortality rate than intermediate species is due to the fact that the body-sizes of species are generally larger the higher they are positioned in the trophic chain, hence they have longer life spans than species below them in the trophic chain (Roff, 1992). The strength of intraspecific competition ($\propto_{ii}$) was randomly drawn from a uniform distribution on the interval -1 to 0. If both *i* and *j* are basal species then α_{ij} gives the strength of direct interspecific competition between basal species which is randomly drawn from a uniform distribution on the interval -0.5 and 0. According to empirical studies (Paine, 1992; Wooton, 1997) predators often prefer one prey species, hence having a larger effect on it than on the other prey species in the food-web. The preferences (h_{ij}-value) of a predator for its different prey species is therefore set to 0.9 for one of the prey species and 0.1 divided by n-1 for the rest of its prey species (see Christianou & Ebenman 2006). The intrinsic attack-rate (β_{ij}) is drawn from a random uniform distribution between -1 to 0. Top predators are allowed to have omnivorous links, meaning that they can feed both on intermediate and basal species. The time it takes for a predator to handle its prey (*T*) was set to 1. The conversion efficiency for omnivorous links was set to 0.02 and 0.2 for consumer-resource links at adjacent trophic levels. Consumer species were not allowed to be without prey since it would not be feasible. Basal species were allowed to be without predators because they still affect the food-web trough direct interspecific competition with the other basal species.

For each set of parameters the model was numerically integrated with the use of an ordinary differential equation build solver (ode23s for stiff system) in Matlab. Initial densities were created through modeling with functional response of type I. After this the system was run over 3000 time steps, if any species population size fell below the extinction threshold (10^{-7}) the community was not considered persistent and therefore rejected. This was done until there were 200 persistent replicate communities. Each species was deleted one at a time from each replicate community and then run for another 20000 time steps. If any species density were to fall below the extinction threshold during this time it was deemed as extinct. After this the deleted species was reintroduced with its changed attributes with a density of 10^{-6}, and then run again for 20000 time steps (Christanou & Ebenman, 2006).

3.2.1. Effects of captivity on species

As mentioned earlier (introduction, 2.3., p.7) a species is affected by captivity in a negative way through mutations and behavioral disorders such as lost hunting-skills or not fearing natural enemies (Swenson et. al., 2001). In this theoretical study the effects of captivity will be portrayed through changes in the reintroduced species mortality-/growth-rate (b_i) depending on whether it is a consumer or a producer species. According to Robert (2009) there is a general fitness decline of up to 40% per generation spent in captivity. However there is large variation in the resulting changes in mortality rates depending on how a species reacts to a relaxed environment such as captivity and what type of reintroduction method that is being used. I therefore use three different scenarios for mortality-/growth-rate changes; a worst-case scenario with a 75% change, one with a 40% change and a best-case scenario with no change at all (0%). In total there will be six model scenarios run using Matlab; three different mortality/growth-rates (0%-, 40%- and 75% change) each executed at two different food-web connectances. Each scenario will have 200 replicates. After the model has been run the results are analyzed by checking how many secondary extinctions there were and the final density of each species.

3.2.2. Community structures

There will be two types of food-webs; one will have a high connectance (0.22) while the other will have a low connectance (0.11). The connectance values are based on what has been observed in natural food-webs (Dunne et al. 2002). The two different connectances are used to see if a higher connectance in an ecosystem causes more changes when species is removed from the food-web compared to a system with low connectance. The connectance in a food-web is calculated through n/S^2 where L is the number of links between consumer- and producer species, n is the number of species in the system. When a species is removed from the food-web through deletion or secondary extinction the resulting connectance changes lead to changed dynamics in the community.

3.2.3. Normalized Euclidian distance

The Euclidian distance is a measure of how much a system changes when it is exposed to perturbations such as species loss or species reintroductions. The parameters used are the initial densities (x) and the densities after the deletion (y) of each species in the food-web. The difference between these two densities is the Euclidian distance in a food-web over a certain time spectrum, i.e. a high Euclidian distance means that there has been a lot of change in the food-web. In figures 3-5 the y-value is taken after the deletion of a species in the food-web. The deleted species densities are not included in the calculation. The data is also normalized making the results more easily comparable. The following formula was used to calculate the normalized Euclidian distance:

$$d_{xy} = \sqrt{\sum_{i=1}^{n} \frac{(x_i - y_i)^2}{{x_i}^2}}$$

3.3. Statistical analysis

To analyze which variable that is most important for a successful reintroduction a classification tree was constructed in Matlab (De'Ath & Fabricius, 2000). A classification tree takes a response variable (reintroduction success) and compares it with a number of predictor variables (in this study; Euclidian distance, number of secondary extinctions and trophic position of species). Classification trees are used for response variables taking binominal values, in this case 1 for a successful reintroduction and 0 for an unsuccessful reintroduction. These binominal numbers are split into two ‘groups’ based on the predictor variables. The predictor variable with most 1’s or 0’s is set as first “split”, meaning that it is the most important factor for the outcome of a reintroduction.

4. Results

In most cases the two different food-web connectances resulted in the same trend, hence they were treated together in some analyses in order to get larger sample sizes.

4.1. Overall patterns

The most important factor for the outcome of a reintroduction attempt is whether the reintroduced species is a producer or consumer species. After this the most important factor when reintroducing a producer species (to the left in figure 2) is how much it has changed due to captivity. However, if a consumer species was reintroduced (to the right in figure 2) the change in its attributes was not the most important factor, they were more sensitive to the change that occurred in the food-web after they were removed from it, hence the Euclidian distance is the most important factor (change in there attributes comes after that).

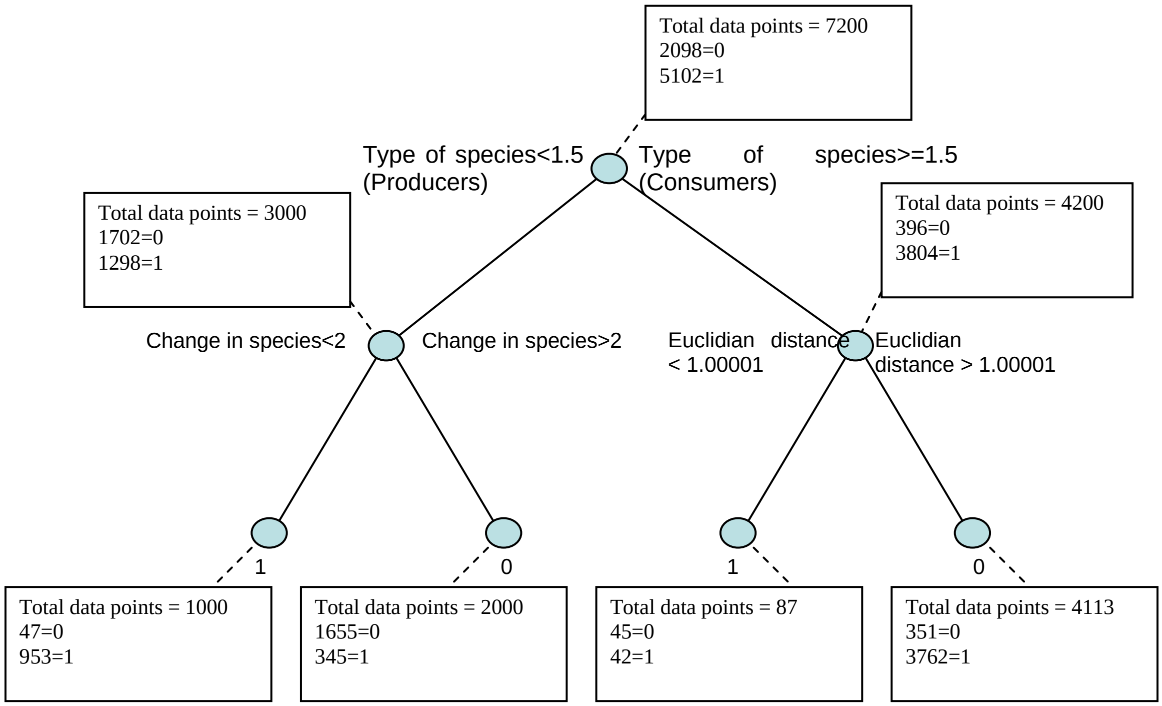

Figure 2. *Classification tree*. 1=Reintroduction success, 0=Reintroduction failure. Here the first split puts basal species to the left and consumers to the right, at this point there is 5102 successful and 2098 unsuccessful reintroductions. Connectance=0.11. This figure is based on 7200 reintroduction attempts.

4.2. Four outcomes

The most important factor for a successful species reintroduction is whether it is a producer or consumer species (fig. 2). There are varying results in reintroduction success and secondary extinctions caused by reintroductions depending on the trophic level of a species and the degree of change in the reintroduced species. The following tables are based on Christanou & Ebenman's (2006) four different outcomes when reintroducing a species presented earlier in the thesis (introduction, 2.3., p.7).

Table 1. *Basal species.* The four outcomes when reintroducing a basal species; I= failure without causing any secondary extinctions, II=failure with secondary extinctions, III=success without secondary extinctions, IV=success with secondary extinctions. This table is based on both connectances with 6000 reintroduction attempts.

Basal species	I: Failure	II: Failure+ secondary extinctions	III: Success	IV: Success+ secondary extinctions
0% Change	0,032	0,017	0,5185	0,4325
40% Change	0,6055	0,095	0,2245	0,075
75% Change	0,8155	0,1365	0,039	0,009

As stated earlier, a basal species has a harder time to reenter the food-web when its growth rate has changed. This leads to less secondary extinctions, since they cannot come back into the ecosystem again causing the rapid increase in case I (table 1 and figure 12).

Table 2. *Intermediate species.* The four outcomes when reintroducing a species; I= failure without causing any secondary extinctions, II=failure with secondary extinctions, III=success without secondary extinctions, IV=success with secondary extinctions. This table is based on both connectances with 4800 reintroduction attempts.

Intermediate species	I: Failure	II: Failure+ secondary extinctions	III: Success	IV: Success+ secondary extinctions
0% Change	0,048125	0,019375	0,845625	0,086875
40% Change	0,10625	0,021875	0,788125	0,08375
75% Change	0,16375	0,0275	0,73125	0,0775

Since the intermediate and top predator species (table 2 and 3) do not have the direct interspecific competition like basal species have, they are more likely to have a successful reintroduction without causing any secondary extinctions. Further, there is a difference how the consumer species react to changed attributes (mortality rates) compared to producer species; there are effects but not as dramatic as in basal species. The data also indicate that there are less secondary extinctions when reintroducing a consumer species then when reintroducing a producer species.

Table 3. *Top predator species*. The four outcomes when reintroducing a species; I= failure without causing any secondary extinctions, II=failure with secondary extinctions, III=success without secondary extinctions, IV=success with secondary extinctions. This table is based on both connectances with 3600 reintroduction attempts.

Top predator species	I: Failure	II: Failure+ secondary extinctions	III: Success	IV: Success+ secondary extinctions
0% Change	0,02	0,006667	0,93	0,043333
40% Change	0,0675	0,0075	0,885833	0,039167
75% Change	0,1175	0,01	0,835833	0,036667

4.3. Reintroduction success and the effects of Euclidian distance

According to the results the reintroduction success increases with increasing Euclidian distance, that is, with increasing structural change in the food-web. This means that the chance of a successful species reintroduction is higher if the densities of the other species in the food-web have changed since the species was removed from it. As can be seen the reintroduction success of consumer species that have been bred in captivity is affected by changes in food-web structure (fig. 4, 5). This is also confirmed by the classification tree (fig. 2) where the Euclidian distance is at the first split for consumer species, hence the most important factor when reintroducing a consumer species. The producer species are also affected by changes in structure of the food-web, however, it is clear that they are more sensitive to changes in their own attributes caused by captivity (fig. 3). This is in line with the results from the classification tree analysis.

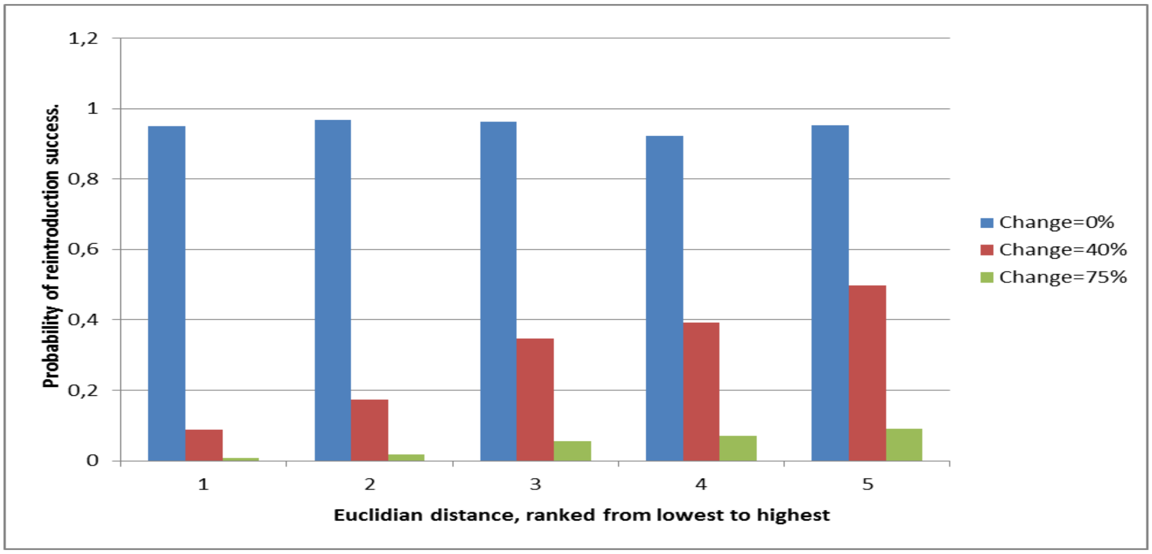

Figure 3. *The probability of reintroduction success of basal species as a function of change in food-web structure (Euclidian distance), ranked from the lowest to the highest Euclidian distance in each food-web.* This figure is based on both connectances with 6000 reintroduction attempts.

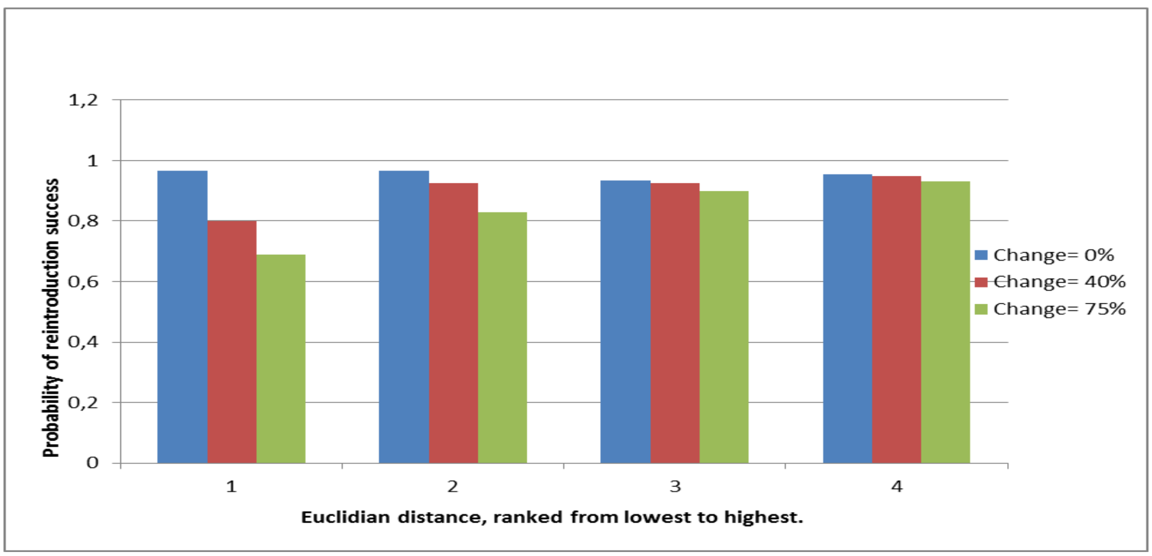

Figure 4. *The probability of reintroduction success of intermediate species as a function of change in food-web structure (Euclidian distance), ranked from the lowest to the highest Euclidian distance in each food-web.* This figure is based on both connectances with 4800 reintroduction attempts.

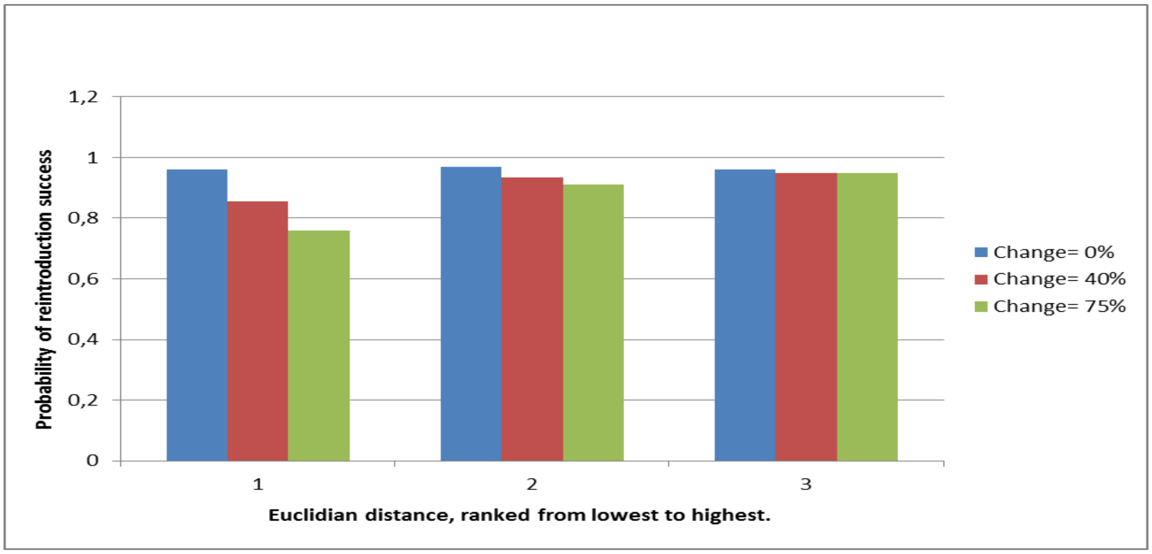

Figure 5. *The probability of reintroduction success of top predator species as a function of change in food-web structure (Euclidian distance), ranked from the lowest to the highest Euclidian distance in each food-web.* This figure is based on both connectances with 3600 reintroduction attempts.

4.4. Reintroduction success and the number of species left in the food-web.

The basal species were most sensitive to the number of species left in the food-web; the probability of successful reintroduction decreased with increasing number of species remaining in the web (fig. 6). In contrast, the consumer species had a higher probability of reintroduction success if there were more species left in the food-web (fig. 7 & 8).

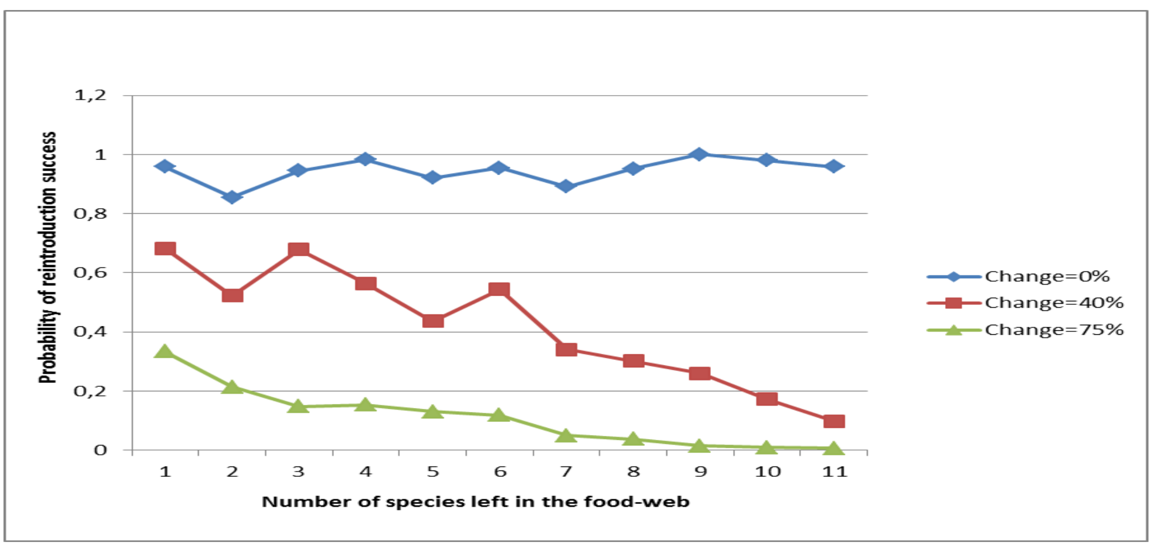

Figure 6. *The probability of reintroduction success as a function of the number of species left in the food-web when reintroducing a basal species*. This figure is based on both connectances with 6000 reintroduction attempts.

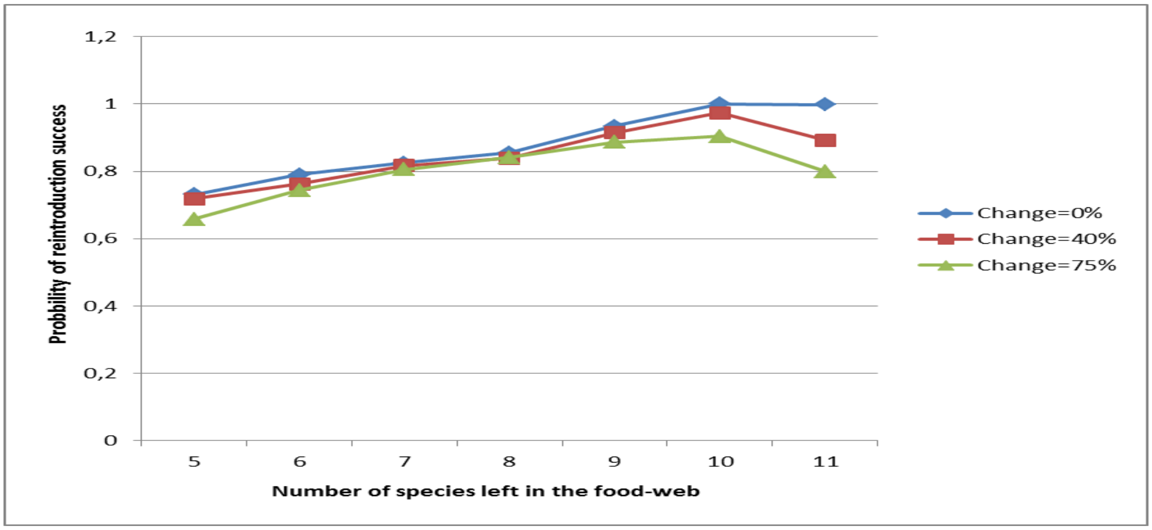

Figure 7. *The probability of reintroduction success as a function of the number of species left in the food-web when reintroducing an intermediate species.* When there were less than 4 species left in the food-web there were too few data point (sample size was too small), hence they were removed. This figure is based on both connectances with 4800 reintroduction attempts.

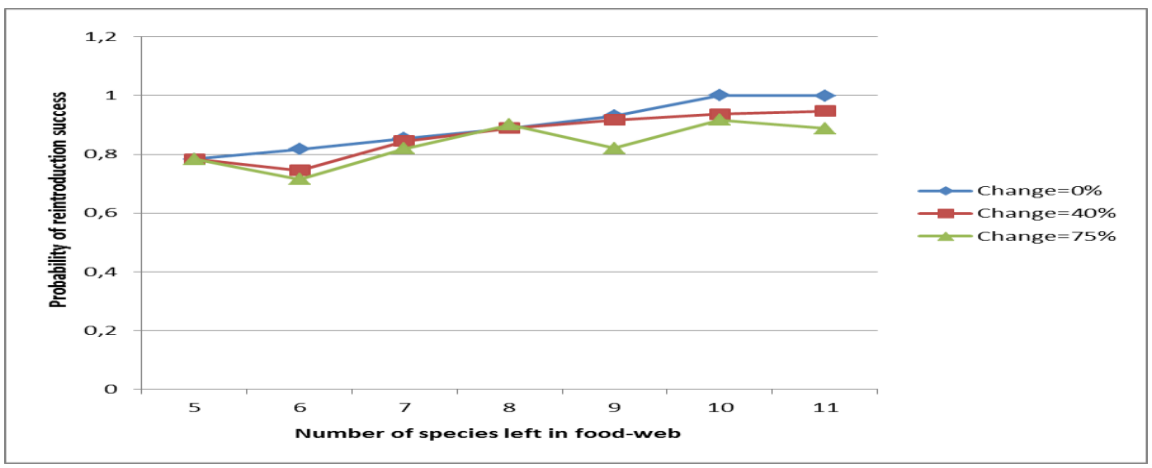

Figure 8. *The probability of reintroduction success as a function of the number of species left in the food-web when reintroducing a top predator species.* When there were less than 4 species left in the food-web there were too few data points (too small sample size), hence they were removed. This figure is based on both connectances with 3600. reintroduction attempts.

4.5. Secondary extinctions caused by reintroduction

The risk of secondary extinctions following a reintroduction is highest when reintroducing a basal species and lowest when reintroducing a top predator. For basal species there is a significant difference in the risk for a 0% change and 40% and 75% change, while this is not the case for consumer species (fig. 9 and 10). The risk for a basal species to cause secondary extinctions when reinvading a food-web is lower if the reintroduced species has changed in captivity.

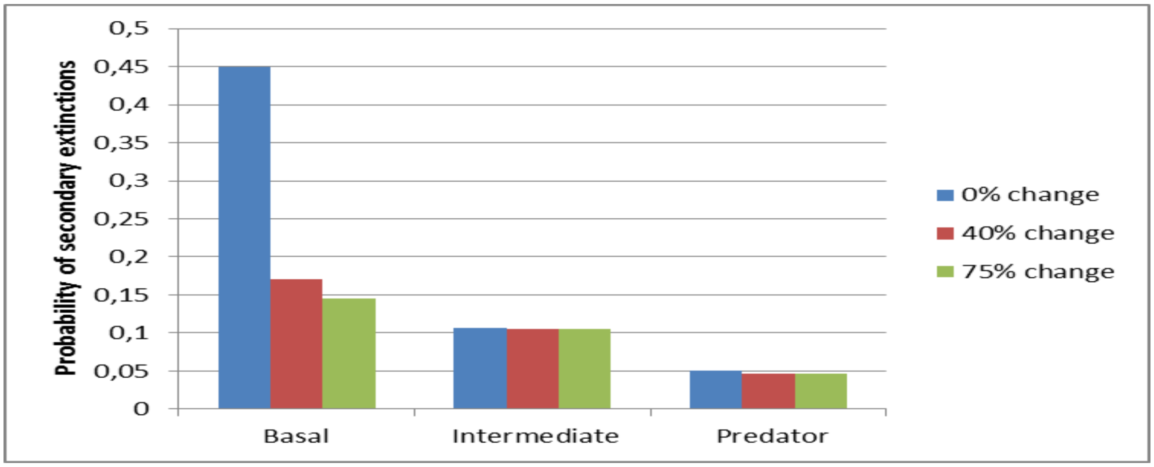

Figure 9. *Secondary extinctions caused by reintroduction of species from the three different trophic levels.* This figure is based on both connectances with 6000 reintroduction attempts.

The number of species going secondarily extinct following a reintroduction was higher in the highly connected food webs (C=0.22) than in the lowly connected webs (C=0.11) (fig. 10).

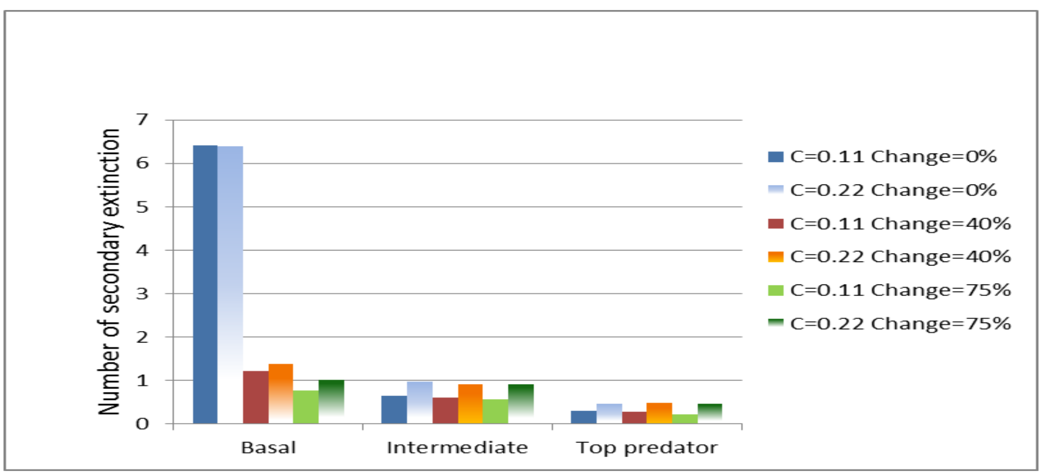

Figure 10. *The number of secondary extinctions due to the reintroduction of species from the three tropic levels.* The bars with a gradient color are the models with a connectance of 0.22.

5. Discussion

5.1. Effects of captivity of species on reintroduction success

5.1.1. Producer species

The results of this study indicate that when reintroducing the producer (basal) species it is most important to look at how much they have changed in their attributes in captivity (classification tree analysis, fig. 2). Reintroduction success of basal species is more sensitive to changes in captivity than is the case for consumer species (see fig. 6 and table 1). The most likely explanation for this is that it is an effect of the direct interspecific competition among the basal species. When there are many species left in the food-web it is harder for the captive-bred basal species with changed attributes to compete against other basal species (fig. 6), although they have a slightly higher chance to succeed if there have been large changes in the food web (fig. 3 and 6). The removal of a species from a food-web can lead to cascade effects causing secondary extinctions (Ebenman et al., 2004). According to the present study a basal species is more likely to reinvade if there are few species left in the food web (fig. 6). When there are few species left in the food web there are also few basal species left, i.e. less competition for the reintroduced species.

5.1.2. Consumer species

As already mentioned in the introduction it is important for studies within the field of reintroduction biology to not only focus on the change in the captive bred species itself but also to consider how the food-web has changed since the extinction of the species (Lundberg et. al., 2000). This is especially important when reintroducing a consumer species since the probability of successful reintroduction of these species is most sensitive to changes in the food-web (fig. 2). Montoya et al. (2006) suggests that the large species in a food-web (mostly consumer species) needs more species to feed upon the larger they are, making them sensitive to a low number of species or large change in the food-web. This is in line with what was observed in the present study where more species left in the food-web meant a higher probability of reintroduction success (figure 7 and 8). However, when the Euclidian distance increases the species seem to be more easily reintroduced compared to when there was less change in the system (a lower Euclidian distance) (fig. 4 and 5). It appears that this contradicts what Montoya et al. (2006) states in their article. However, a relatively large change in the ecosystem (i.e. a high Euclidian distance) does not necessarily mean a lower number of species for the consumers to prey on. It could just mean that one producer species decreases in size will the other takes its place and also the place as main-prey for a consumer species.

Another factor that is important for the success of a reintroduction is the number of individuals that is reintroduced. The number of individuals available for reintroduction depends on the length of time the species has been kept in captivity. It has been suggested that there is an optimal time of 10-20 generations kept in captivity before a species should be reintroduced (Robert 2009 and Theodorou & Couvet, 2004). It is hard to confirm this theory through the results of this study. However too long time spent in captivity (75% change) leads to a lower chance of a successful reintroduction meaning that the species should be kept in captivity for as short time as possible (also stated by Frankham, 2008). Nevertheless, the conclusion made by both Robert (2009) and Theodorou & Couvet (2004) that there is a higher chance of reintroduction success if you release more individuals back into the wild cannot be neglected, and it is obvious that there will be more individuals available the longer the species have been kept in captivity. Aaltonen et al. (2009) also brings up another aspect of this in their article on Vancouver marmots, which concludes that individuals that has spent their first two years in captivity has a larger chance to survive in the wild compared to the yearlings. Thus, in some cases it could be beneficial for a species to spend some more time in captivity although this is more of an exception than a general rule. Based on the results from this study there should be a certain “optimal time” spent in captivity as Robert (2009) and Theodorou & Couvet (2004) states. There should be time to bred enough animals to have a good chance of a successful reintroduction, but time in captivity should be as short as possible so that changes in the attributes of species is not so large as to profoundly reduce the chance of reintroduction success (table 2 & 3).

5.2. Changes in the food web structure caused by species loss and reinvasion

Ebenman et al. (2004), Eklöf & Ebenman (2006) and Christianou & Ebenman (2006) found that effects on the food-web were most pronounced if a basal (producer) species was removed/reintroduced. This is also observed in the results from this study (fig. 9); the effects on the food-web are largest when a basal species is lost and reintroduced, in this sense it is a bottom-up controlled food-web (fig. 9 and 10). A possible explanation for this is that the consumer species in the food-web are directly and indirectly dependent on the existence of a producer species in order for them to get enough food to survive. On the other hand the producer species can still survive even if a consumer species disappears, although there might be some secondary extinctions and shifts in the community structure. Yet again the effect of captivity is very pronounced in basal species (table 1). Specifically, they will affect the food web less if their attributes have changed a lot due to captivity, making it harder for them to outcompete other basal species when reinvading.

There are different theories why food webs react to species loss in different ways depending on from which trophic level you remove a species. Montoya et al. (2006) writes in their article that it is always hard to predict which species that is going to affect the food-web the most. There are indirect interactions between species making it very hard to fully understand how the ecosystems will respond to species losses. Dunne & Williams (2010) discuss in their article that the robustness of a food web is dependent on species richness and connectance. Higher connectance means a more robust food web less sensitive to perturbations such as species removal.

5.3. Food-web connectance

Eklöf & Ebenman (2006) conclude in their study that the connectance of a food-web is an important parameter for the outcome of a species removal. A highly connected community is more sensitive to the loss of top consumer species than a lowly connected community, while it is more robust to removal of basal and intermediate species. The connectance of a food-web will also determine the success of an invasion or reintroduction (Baiser et al. 2010). For a food web with a given number of species higher connectance means more links within the web. Baiser et al. (2010) found that connectance was the best predictor for basal, herbivore (intermediate) and omnivore species invasion success. For the carnivores (top predators) the best predictor for invasion success was the proportion of herbivores in the food web. It is also important to which trophic level the invasive species belongs. If the invasive species has a lot of predators it is harder for the species to invade, while if it has many species to prey upon it is more likely to succeed. This is also observed in the present study; the reintroduction success decreases for producer species and increases for consumer species with increasing number of species in the food web (figure 6, 7 and 8). Romanuk et al. (2009) found in their study that the most important factor for invasion success is whether a species is a generalist (feeding on many prey species) or not.

In the present study the role of food web connectance has not been studied to any further extent, however it was found that the response of a food web to species reintroduction depends on its connectance. A higher connectance gives a higher risk of causing secondary extinctions when a species is reintroduced, meaning that a highly connected food web is more sensitive to this kind of perturbation than one with low connectance. These results appear to contradict what Dunne & Williams (2010) wrote in their article. However, they were dealing with the response of food webs to species loss and not with their response to species inavasion.

6. Recommendations and future directions

When reintroducing a species from captivity there is a number of things that can be done to enhance the chance of a reintroduction success. Of course it is important to remove the initial cause of extinction before reintroducing a species (Fisher & Lindenmayer, 2000). However, with this study in mind it is also important to reduce the negative effects of captivity as much as possible. Araki (2007) and Frankaham (2008) suggest that the captive population should continually be reinforced with animals from the wild in order to maintain genetic diversity and minimize behavioural disorders. There is a need for monitoring of genetic effects when reintroducing species; Laikre et al. (2010) suggests that there should be a risk-benefit tradeoff between the genetic effects and economic and social gains when reintroducing a species, especially when there is a commercial interest in the reintroduction/enhancement of a population. The method for the reintroduction itself should also be carefully considered in order to maximize the reintroduction success and minimize negative effects on the target food-web (Bryant & Reed, 1999; Faria et al. 2010; Wallace & Temple 1987). Faria et al. (2010) for example exposed captive bred guppies to their natural occurring enemies, in this case parasites, before they were released. As a result he guppies became resistant to the parasites in the wild, leading to a more successful reintroduction.

The present study deals with how changes in the growth and mortality rates of species affect the probability of successful reintroduction. It would also be interesting to study how the outcomes of reintroductions would be affected if the interaction strengths between species were to be changed. This includes changes in the ability of consumers to find and catch prey and the ability of prey to detect and hide from predators. These are abilities that can be negatively affected by a life in captivity. Such changes are also likely to have large effects on the outcome of reintroduction attempts.

7. Concluding remarks

The results from this study show that species with changed attributes due to captivity has a harder time to reestablish themselves in a food-web, especially so for basal species. The effects of a reintroduction on the community are correlated to how much the attributes of a species has changed. A larger change means less negative effects on a community such as secondary extinctions and cascade effects. Also changes in the food web affect the reintroduction success. The loss and reintroduction of basal species affect the food-web more than loss and reintroduction of species at higher trophic levels.

Thomas et al. (2010) writes that captive breeding is only a way to be treating the symptoms rather than the actual cause of the species decline. Captive breeding should be seen as a last option in conservation biology only to be used if there are no other options left. There is always an ecological risk when reintroducing species, they can erode biodiversity and disrupt the functioning of ecosystems (Ricciardi & Simberloff 2009). The ideal *ex situ* conservation management would be to allow natural selection to work with as little interference from humans as possible. Is *ex situ* conservation biology too "human" in today's zoos? Does it actually cause more problems for the future of a species when they are held in such a relaxed environment where natural selection is absent (Bryant & Reed, 1999)? However, this is a last resort solution that gives us a chance to preserve and reintroduce species back into the wild. At least it is better than not having the species at all.

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