

Department of Physics, Chemistry and Biology

Master Thesis

# Reintroducing captive bred species – a community ecological perspective

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<b>Sammanfattning</b> 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. Zoo's that originally was created as an amusement park for people has today gotten 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 up to 40% per generation in captivity. A reintroduction of a species that is bred in a zoo will lead to a decreased reintroduction success the longer time it is 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 (are likely) 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) effects a food-web and what risks there are in reintroducing it. A Lotka-Volterra model of type II functional response is used. This is computed through the program Matlab with three different types of 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 was most sensitive to the change in its attributes due to the direct interspecific competition built in to the model, whilst consumer species were more sensitive to change in the food-web (Euclidian distance). The producer species was found to cause most secondary extinctions in all scenarios, hence meaning that it is a bottom-up controlled food-web. The present study suggests that the success of a reintroduction attempt is affected by both changes in the food web and the change in the species itself. <p style="text-align: right;">2</p>
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<b>Nyckelord</b> Keyword Captive breeding, reintroductions, species interactions, food-web, secondary extinctions, Lotka-Volterra models.
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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. Zoo's that originally was created as an amusement park for people has today gotten 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 up to 40% per generation in captivity. A reintroduction of a species that is bred in a zoo will lead to a decreased reintroduction success the longer time it is 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 (are likely) 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) effects a food-web and what risks there are in reintroducing it. A Lokta-Volterra model of type II functional response is used. This is computed through the program Matlab with three different types of 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 was most sensitive to the change in its attributes due to the direct interspecific competition built in to the model, whilst consumer species were more sensitive to change in the food-web (Euclidian distance). The producer species was found to cause most secondary extinctions in all scenarios, hence meaning that it is a bottom-up controlled food-web. The present study suggests that the success of a reintroduction attempt is affected by both changes in the food web and the change in the species itself.

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

## **2. Introduction**

Through history, species has disappeared from their natural ranges due to anthropogenic activities. Although mankind has introduced species into the wild for over a millennia, it is only for 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 conservation 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 habitat is being destroyed due to anthropogenic activities the only option is to capture a part of or in the worst case scenario the whole population of a species and take it 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 has shown that the reintroductions of captive bred species has 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 captive bred species attributes (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/generation. The reasons for this are mainly due to genetic deterioration and behavioral disorders. The evolutionary aspect 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 the 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, optimal is 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 get a successful reintroduction (Frankham, 2008). The general 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 and a long time means large population with 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 zoo’s 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, 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 is a few secondary extinctions or none at all (Ebenman & Jonsson, 2005). Since empirical studies (for obvious reasons) are hard to conduct the use of theoretical modeling are 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 link between species is essential when it comes to how other parts of an ecosystem react to extinctions. The link-strength is not the only vital parameter if species are removed from an ecosystem, for example species richness and connectance is vital when it comes to the robustness of a food-web (Ebenman et. al., 2004). For example, if there are few connections between species in a food-web, the chances of secondary extinctions are much higher compared with ecosystems with many connections (Dunne & Williams, 2009. Eklöf & Ebenman, 2006). Christanou & Ebenman (2006) list four possible different outcomes when a species is reintroduced into a food-web (see fig. 1).

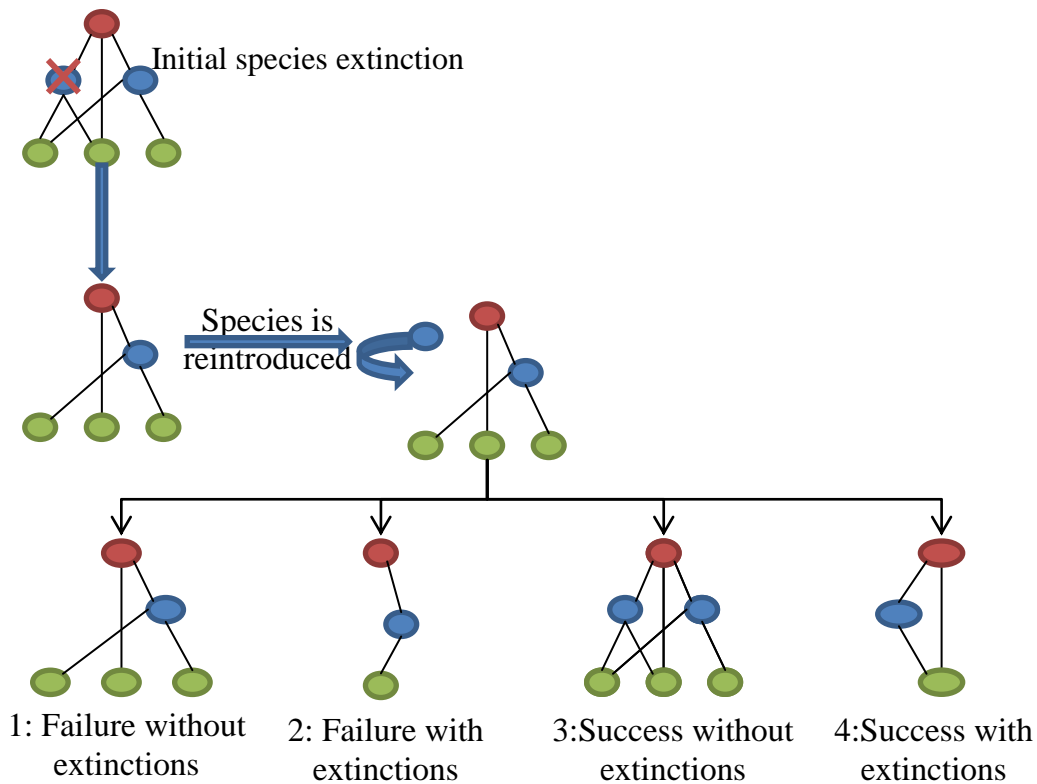


Fig 1. Four potential outcomes of a species reintroduction I) The system or the species itself has changed too much for the reintroduced species to survive in the system, II) The reintroduced species can survive for a while but cause secondary extinctions and in the end goes extinct itself. III) The 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 compete out other species in the food-web causing secondary extinctions (from Christianou & 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 further damage and secondary extinctions, especially if there were secondary extinctions when the species initially disappeared. 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 the hunting, foresting or fishing industry where enormous amounts 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. Studies have been conducted on the success-rate of reintroduction, reintroduced species born in captivity and their chances of success. 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 due to the time spent in 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 (one at a time) in order to estimate what impact their disappearance has on the food web. These species will have different attributes and functions in the system.

### 3. Methods

The method used in this thesis was mainly mathematical modeling performed in the program Matlab. The analyses based on Christianou & Ebenmans (2006) deterministic food-web models which they used for reintroducing species into communities. The model community that was generated is a triangular shaped deterministic 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-sample 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. In order to model the dynamics of the model food-webs the Lotka-Volterra equations were used. Two types of functional responses were used; type I when constructing the food-web and type II when modeling the food-web.

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

The general Lotka-Volterra equation;  $dx_i/dt$  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  $\alpha_{ij}$  which is the per capita effect that species  $j$  has on species  $i$ :s per capita growth rate.



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

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

Equation (2) shows how the  $\alpha$  in the Lotka-Volterra equation works in 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 ( $\alpha$ ) of the predator on the prey is dependent on the population size of the prey species.  $\beta_{ij}$  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 will be three different trophic levels in this model; basal, intermediate and top predator species. The basal species will 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 -0.001. The time it took for a predator to handle its prey ( $T$ ) was set to 1. The intraspecific in the model ( $\alpha_{ii}$ ) is randomly drawn from a uniform distribution of -1 to 0. If both  $i$  and  $j$  is a basal species then it gives the interspecific competition between basal species which also is randomly drawn from a uniform distribution of -0.5 and 0. According to empirical studies (Paine, 1992; Wootton, 1997) the predators is set to favor one prey species, hence having a larger effect on it than the other prey species in the food-web. The  $h_{ij}$ -value for a predator is therefor set to 0.9 for one random consumer-prey and 0.1 for all the other prey species in the system. These were set according to the method that Christianou & Ebenmans (2006) used in their study. 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 these species are generally larger the higher you come into the trophic chain, hence they have longer life spans than species below them in the trophic chain (Roff, 1992). The intrinsic attack-rate ( $\beta_{ij}$ ) 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 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 interspecific competition with the other basal species.

Each set of parameters 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 seen 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 up to 40% per generation spent in captivity, logical would be to increase/decrease the mortality-/growth-rate with 40% at each reintroduction. However this differs a lot depending on what type of reintroduction method that is being used, how a species reacts to a relaxed environment such as captivity etc. The best way would be to have a best-case scenario and a worst-case scenario where mortality-/growth-rate changes differently, one case-scenario with a lot of change (75%) and one with none at all (0%). In total there will be six model scenarios run in Matlab, three different mortality/growth-rates (0%-, 40%- and 75% changed attributes) each executed with two different connectances. Each scenario will have 200 replicates.

After the model has been run the results is analyzed by checking how many secondary extinctions there was and the final density of each species.

### **3.2.2. Community structures**

There will be two types of food-webs; the first one will have a higher connectance (0.22) whilst the second one will have a lower connectance (0.11). The connectance-values are based on what is observed in empirical food-webs (Baiser et. al. 2010). 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  $L/S^2$  where  $L$  is the number of links between consumer- and producer species,  $S$  is the number of species in the system. When a species is removed from the food-web through deletion or secondary extinctions the connectance changes leading 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 a species of the 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. Statistic 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 case; Euclidian distance, number of secondary extinctions, the initial density of the species and trophic position of species. The classification tree is a binominal tool that either gives 1, meaning a successful reintroduction or 0 meaning an unsuccessful reintroduction. These binominal numbers is split in two based on the predictor variables. The predictor with most 1 or 0 is set as first “split” that is the most important factor for a reintroduction.

## 4. Results

In most cases the two different connectances resulted in the same trend, hence both of them was put together in some graphs in order to get more data points.

### 4.1. Overall patterns

The most important factor for the outcome of a reintroduction attempt is whether it is a producer or consumer species. After this the most important factor if you reintroduce a producer-species (to the left in figure 2) is how much change it has in its attributes from 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).

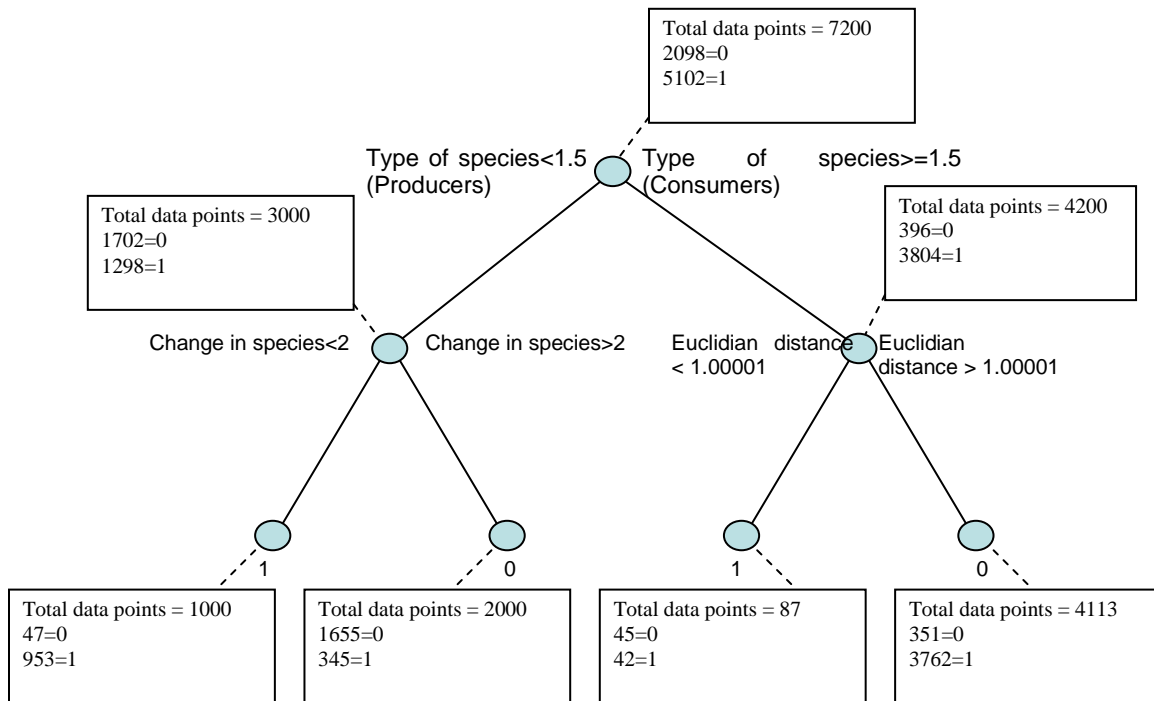


Figure 2. *Classification-tree*. Connectance=0.11. 1=Reintroduction success, 0=Reintroduction failure. E.g. the first split puts basal species to the left and consumers to the right, at this point there is 5102 successful and 2098 unsuccessful reintroductions. This figure is based on 7200 reintroduction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

## 4.2. Four outcomes

The most important factor for a successful 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 trophic level when increasing the change in the reintroduced species. The following tables are based on Christanou & Ebenmans (2006) four different outcomes when reintroducing a species presented earlier in the thesis (introduction, 2.3., p.7).

Table 1. *Basal species: Four different outcome*). 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 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, the basal species has a harder time to come back into the food-web when it is reintroduced with changed growth-rate. This leads to less secondary extinction, 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 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 as basal species has, they are more likely to have a successful reintroduction without any secondary extinctions. Further there is a difference how the consumer species reacts to changed attributes compared to producer species, the effects exists 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. *The four outcomes when reintroducing a species, Top predator 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 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 reintroductions success increases when you have a higher Euclidian distance. This meaning that the chance of a species reintroduction is higher if the food-web has changed a lot since the species were removed from it. The results for reintroduction success depending on the Euclidian distance of each food-web shows that there is a slight tendency that the consumer species are more sensitive to a higher Euclidian distance when reintroduced from captivity (fig. 3, 4). 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 is also sensitive to changes in the food-web, however it is clear that they are more sensitive to change in the species attributes (fig. 3).

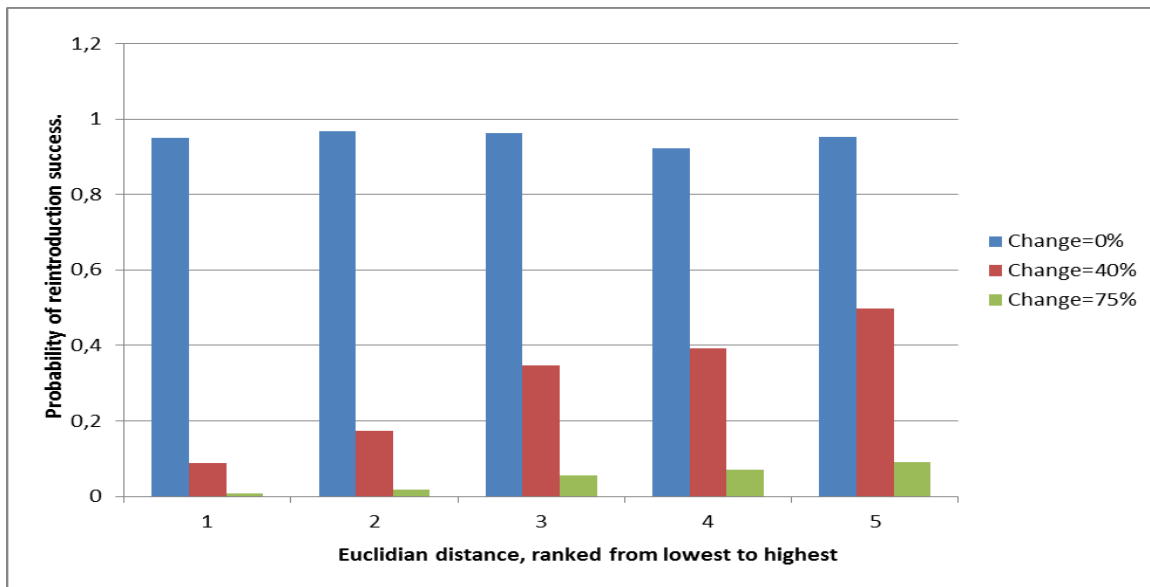


Figure 3. *Basal species.* The probability of reintroduction success depending on the Euclidian distance in the food-webs, ranked from the lowest to the highest Euclidian distance in each food-web. This figure is based on both connectances with 6000 reintroduction attempts.

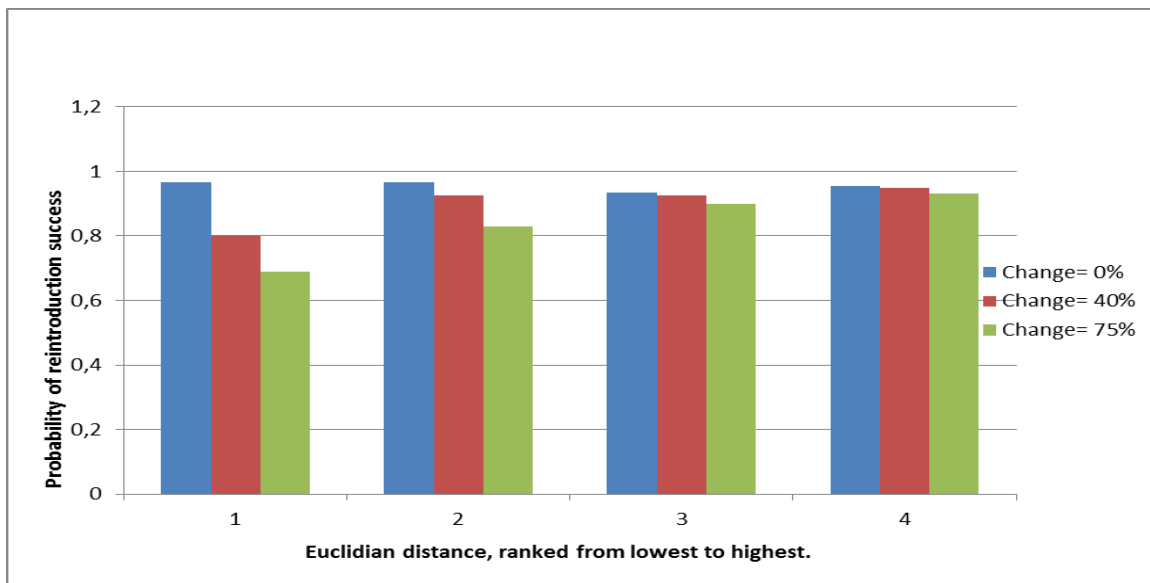


Figure 4. *Intermediate species.* The probability of reintroduction success depending on the Euclidian distance in the food-webs, ranked from the lowest to the highest Euclidian distance in each food-web. This figure is based on both connectances with 4800 reintroduction attempts.

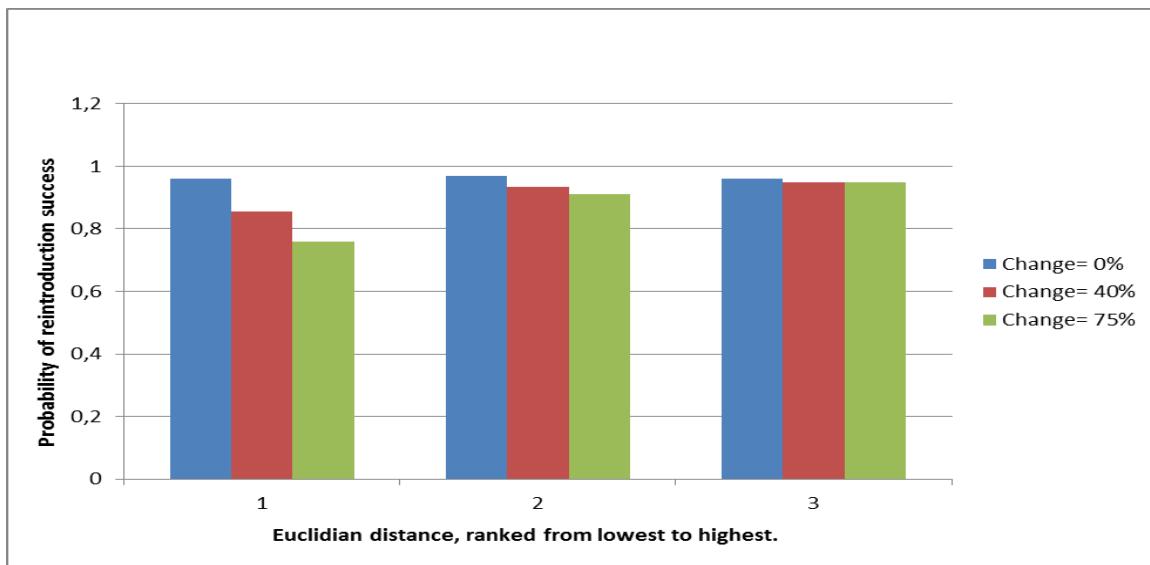


Figure 5. *Top predator species.* The probability of reintroduction success depending on the Euclidian distance in the food-webs, top predator species, ranked from the lowest to the highest Euclidian distance in each food-web. This figure is based on both connectances with 3600 reintroduction attempts.

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

The basal species was most sensitive to how many species there are left in the food-web when they are reintroduced (fig. 6). The consumer species has a higher probability reintroduction success if there are more species left in the food-web (fig. 7 & 8).

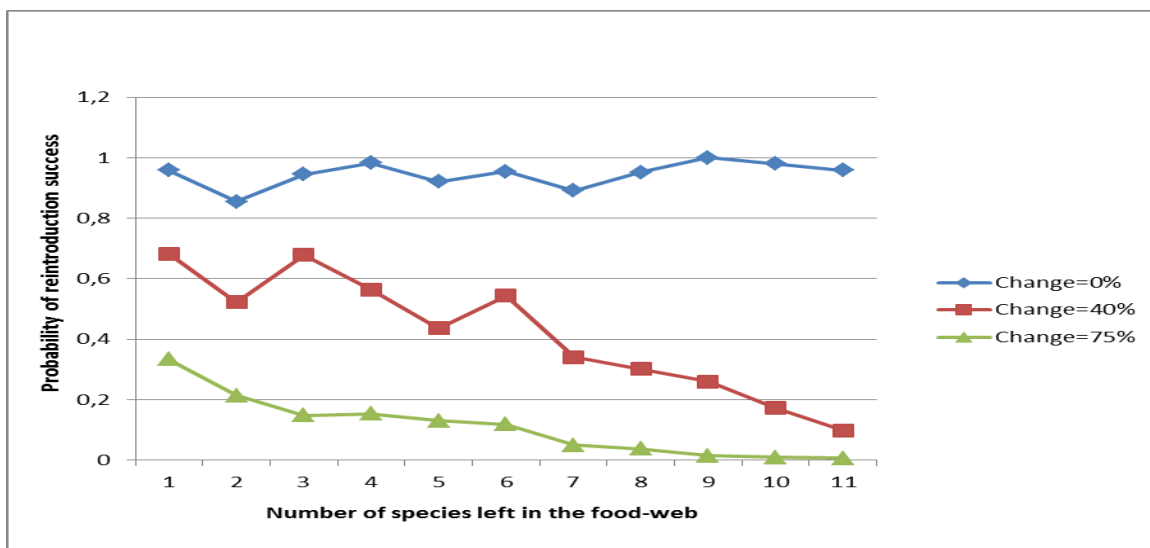


Figure 6. *Basal species.* The probability of reintroduction success depending on how many species that is left when reintroducing a basal species. This figure is based on both connectances with 6000 reintroduction attempts.

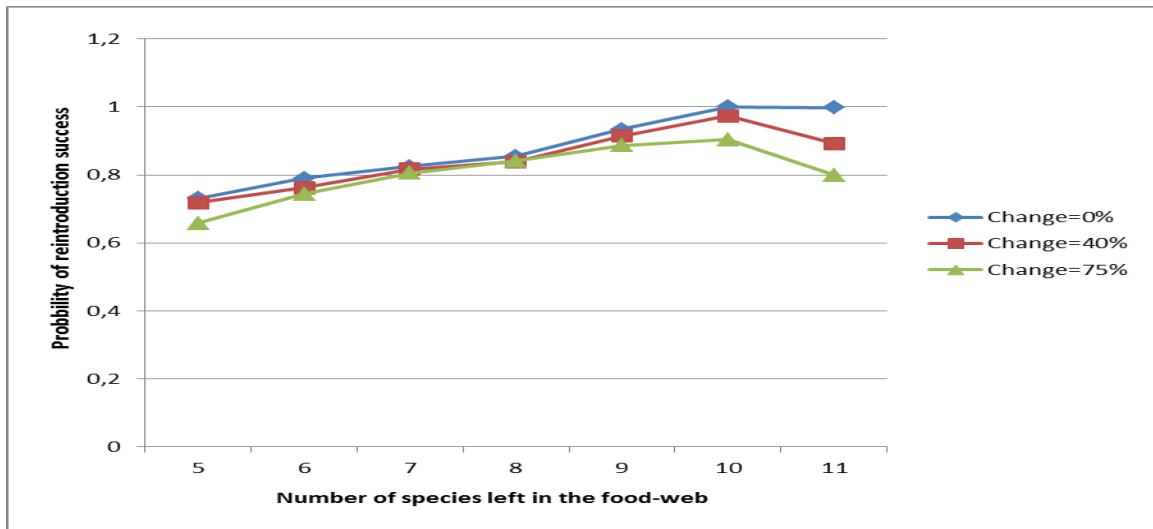


Figure 7. *Intermediate species.* The probability of reintroduction success depending on how many species that is left when reintroducing an intermediate species. When there was less than 4 species left in the food-web there were too few data points, hence they were removed. This figure is based on both connectances with 4800 reintroduction attempts.

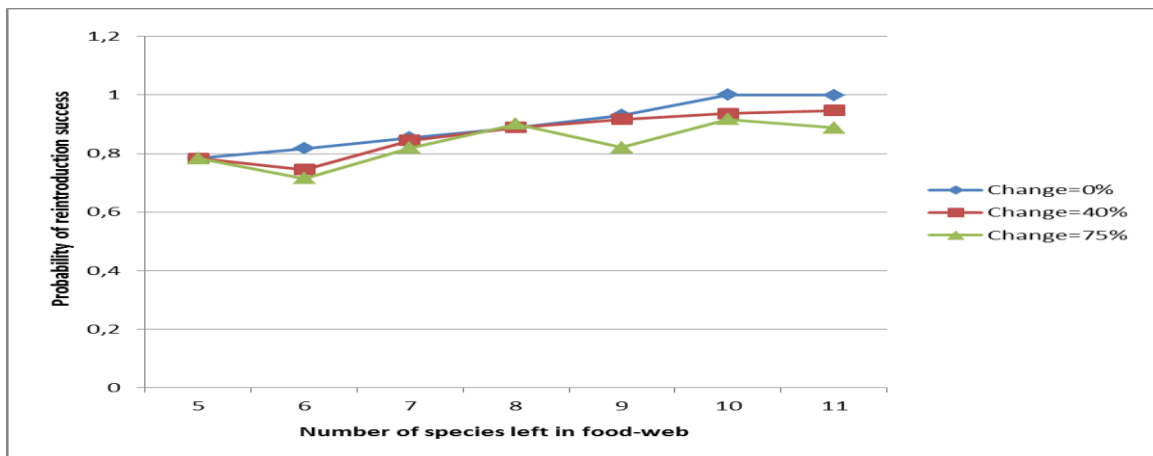


Figure 8. *Top predator species.* The probability of reintroduction success depending on how many species that is left when reintroducing a top predator species. When there was less than 4 species left in the food-web there were too few data points, hence they were removed. This figure is based on both connectances with 3600 reintroduction attempts.



#### 4.6. Secondary extinctions caused by reintroduction

It is almost inevitable to avoid secondary extinctions, however there can be more or less secondary extinctions depending on the parameters in the model. For producer species there is a significant difference between a 0%, 40% and 75% change, this is not the case for producer species (fig. 9 and 10).

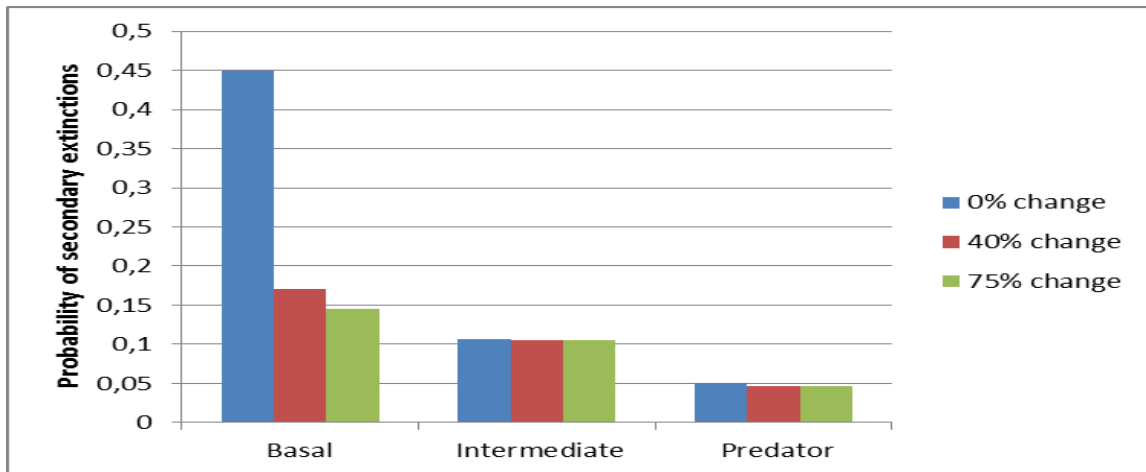


Figure 9. Secondary extinctions due to reintroduction divided into three different trophic levels. This figure is based on both connectances with 6000 reintroduction attempts.

The absolute numbers of species going secondary extinct in the 0.22 connectance-model was in all cases higher than when the model with 0.11 connectance (fig. 10), except for 0% change; basal species. The risk for a basal species causing secondary extinctions is mitigated the more change you add to the reintroduced species, this is also the case for the other two trophic levels.

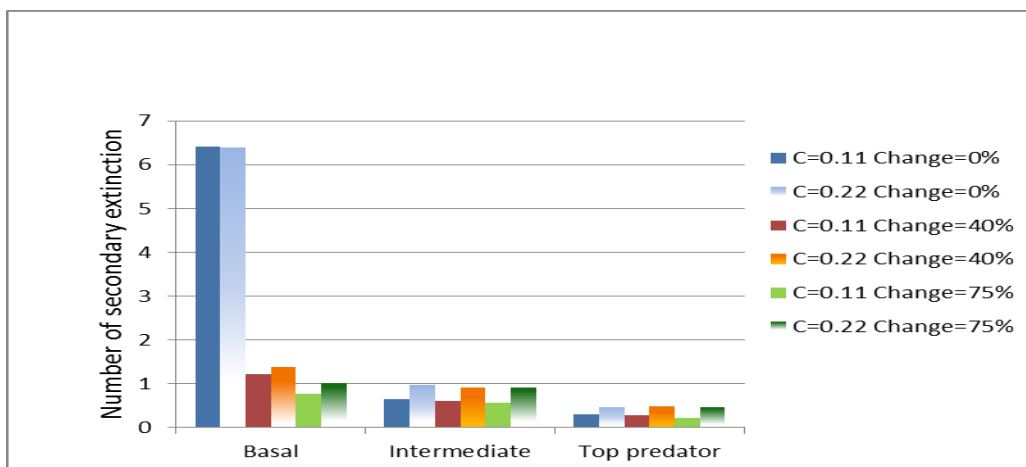


Figure 10. The number of secondary extinctions/ replicate due to the reintroduction of a species, divided into trophic levels. In this figure the same setup as in figure 9 is used, except with absolute numbers instead of percentage. The bars with a gradient color are the models with a connectance of 0.22.

In figure 9 and 10 it is clear that the removal and later reintroduction of basal species has the largest effects on the food-web. However relative to intermediate and top predator species, the basal species effect on how the ecosystem reacts to its reintroduction decreases, as changed attributes from captivity increases.

## **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 species it is most important to look at how much they have changed in their attributes in captivity, according to the classification tree (fig. 2). Out of the three different trophic levels the basal species is the most sensitive to changes in captivity (see fig. 6 and table 1). The most likely explanation for this is that it is an effect of the direct interspecific competition in for producer species. When there are more 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 a lot of changes in the food web (fig. 3). The removal of a species from a food-web can lead to cascade effects causing secondary extinctions (Ebenman et al., 2004). According to the results a producer species is more likely to have a successful reintroduction if there are few species left in the food web (fig. 6). A possible explanation for this could be the direct interspecific competition links built into the model. 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 reintroductions from captivity to not only focus on the change in the captive bred species itself but also 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 they are sensitive to changes in the food-web (fig. 2). Montoya et. al. (2006) suggests is that the large species in a food-web (mostly consumer species) needs more species to feed the larger they are, making them sensitive to a low number of species or large change in the food-web. This is something that was observed in figure 7 and 8 where more species in the food-web meant a higher probability of reintroduction success. However when looking at the result of this study, when the Euclidian distance increases the species seems 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 change in the ecosystem does not necessarily mean a lower amount 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, hence showing a higher Euclidian distance.

Another factor that is important for the success of a reintroduction is the number of individuals that is reintroduced. There is an optimal general time of 10-20 generations kept in captivity before the 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, since it is obvious that there will be more individuals the longer you have them 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. In some cases it could be beneficial for a species to spend some more time in captivity, however this is more of an exception than a general rule. Based on the results from this study there has to be a certain “optimal general time” spent in captivity as Robert (2009) and Theodorou & Couvet (2004) states. When there has been bred enough animals to have a good chance of a successful reintroduction, but they have been in captivity as short time as possible so that the change in their attributes is not too pronounced to decrease the chance of reintroduction success (table 2 & 3).

## **5.2. Changes in the food web structure caused by species loss**

Ebenman et al. (2004), Eklöf & Ebenman (2006) and Christianou & Ebenman (2006) found that there are most effects on the food-web if you remove/reintroduce a basal (producer) species; this is also observed in the results from this study (fig. 9). The effects on the food-web are the largest when you reintroduce a producer species, 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 is 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 shifts in the community structure and secondary extinctions. Yet again the effects of captivity are very pronounced in basal species (table 1). This means that they affect the food web less if they have highly changed attributes due to captivity, making it harder for them to compete with other species.

There are different theories in why the food web reacts to species loss in different ways depending on from which trophic level you remove a species from. Montoya et al. (2006) writes in their article it is always hard to predict which species that is going to affect the food-web the most. There are indirect links between each species making it very hard to fully understand how the ecosystems functions. 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 and reintroductions.

### 5.3. Connectance

Eklöf & Ebenman (2006) conclude in their study that the complexity (connectance) of a food-web is an important parameter to the outcome of a species removal. A complex community is more sensitive to the loss of top consumer species, although it is more robust to species removal. The connectance in a food-web is according to Baiser et al. (2010) what determines the success of an invasion or reintroduction. They calculate the connectance with the number of links (L) and how many species there is in the food web (S) through the formula  $C=L/S^2$ . Thus a higher connectance means more links within a food-web. Baiser et al. (2010) writes in their article that connectance is the best predictor for basal, herbivore and omnivore species invasion success. For the carnivores the best predictor for invasion success is the proportion of herbivores in the food web. It is also important on which trophic level the invasive species is on. If the invasive species has a lot of predators it is harder to succeed, if it has many species to prey on it is more likely to succeed the invasion. This is also observed in this study as seen in figure 6, 7 and 8 where the reintroduction success decreases for producer species and increases for consumer species with the number of species in the food web.

Romanuk et al. (2009) found in their study that the most important factor for invasion success is whether the species is a generalist or not. Once the species is established in the food web the most important factor that distinguished the successful from the unsuccessful was which trophic level the species was on. Lower trophic levels have a higher chance of success, something that is consistent with the results of this study (table. 1, 2 and 3).

In this study the effects of connectance on communities has not been studied to any further extent, however in figure 10 it is obvious that it affects the food-web when reintroducing a species. A higher connectance gives a higher risk of causing secondary extinctions when a species is reintroduced, meaning that a higher connectance food-web is more sensitive to this kind of perturbation than one with low connectance. However, these results appear to contradict what Dunne & Williams (2010) wrote in their article.

In contradiction Fowler & Lindström (2002) found that increased complexity in a community such as changed community size will make the food-web less robust to perturbations such as removal and reintroduction of a species. Although this has not been the main focus of the present study, the results in figure 10 support Fowler & Lindström (2002), a higher connectance, more links in the food-web hence higher complexity, gives more secondary extinctions when a species is reintroduced.

### 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 decline before reintroducing a species (Fisher & Lindenmayer, 2000). However with this study in mind it is also important to reduce the effects of captivity as much as possible. Araki (2007) and Frankham (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, this specially when there is a commercial interest in the reintroduction/enhancement of 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 food-web (Bryant & Reed, 1999; Faria et al. 2010; Wallace & Temple 1987). Faria et al. (2010) for example exposed the captive bred guppies for its natural occurring enemies, in this case parasites, before they are released. The guppies became resistant to the parasites in the wild, hence a more successful reintroduction.

The complexity of a food-web, as discussed by Fowler & Lindström (2002) would be interesting to study further. For example study how the ecological community reacts to a reintroduction if the interaction-strength were to be changed, added stochasticity to the model, changed attack-rates of consumers or other altered parameters, would it cause more or less secondary extinctions in the food-web? Also how the size and structure of a food-web would affect the outcome of a reintroduction. It would further be interesting to see if there are any cascade effects of a reintroduction, why the food web is bottom-up or top-down controlled and determine what parameter that is most likely to cause these effects.

## **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 basal species. The effects on the community are correlated to how much change a species has in its attributes when reintroduced. A higher change means less negative effects on a community such as secondary extinctions and cascade effects. Changes in the food web also affect the reintroduction success. The removal and reintroduction of a basal species affects the food-web most of all three 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 ecosystems (Ricciardi & Simberloff 2009). The ideal ex situ conservation management would be to allow natural selection to take place and as little interference from humans as possible. Are the ex situ conservation biology too “human” in today’s zoo’s, actually causing more problems for the future of a species when they are put in such a relaxed environment where the natural selection is neglected (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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