The Impact of the Absence of Tourism on Colonies of Murres

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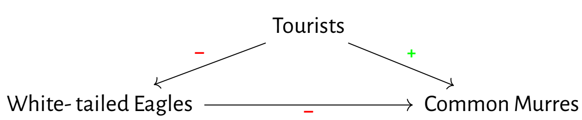
The absense of human visitors during the Covid-19 pandemic has set off an unprecendented chain of disturbances in a colony of common murres (*Uria aalge*) in the Stora Karlsö natural reserve off the southeastern coast of Sweden. In this paper we model these disturbances and their consequent effect on the colony. Our investigations suggest that prolonged restrictions on tourism would be detrimental to the survival of murres.

Covid-19 | Social-Ecological system | Murres | Eagles

The Covid-19 pandemic has presented us with a plethora of new challenges. The disease has disrupted the way of life of various living organisms around the globe and has also reshaped their ecosystems. In this paper, we analyze the impact of the abscence of tourists on a population of common murres living on the island of Stora Karlsö, Sweden, with a desire to predict the effect on the population of murres over the next few years.

As discussed in [Hentati-Sundberg et al. (2021)], there is evidence suggesting that the absence of visitors in Stora Karlsö is promoting a higher-than-usual presence of white-tailed eagles (*Haliaeetus albicilla*) near the commom murres' colonies. [*] Consequently, since murres are known to be instinctively afraid of the eagles, they become agitated and scatter away upon sighting them. These more frequent disturbances caused by a higher population density of the white-tailed eagles in the area contribute to ***i)*** eggs being left unprotected, ***ii)*** loss of a portion of the unhatched eggs during the agitations caused by the eagles (murres kick the eggs off the ledge or destroy them amidst the chaos caused by sighting of the eagles), and ***iii)*** the murres mating less than usual. The overall effect of these disturbances created by the ever-growing presence of eagles is causing a diminution in the population of newborn murres. The following diagram summarizes the positive (+) or negative (−) effects that each of the participants (tourists, murres, and eagles) has on one another.



The situation, however, is much more complex than the simple scenario depicted above. For instance, it is known that the eagles tend not to attack the murres or their eggs directly. Rather, it is their indirect effect at causing the murres to abandon their eggs out of fear that leads to major losses for the murres' population, since the eggs are then left unprotected and prone to attack from predators such as seagulls and crows. [Hentati-Sundberg et al. (2021)] While there have been reports of eagles harassing the murres, these occurrences are considered rare, and thus will be ignored in our model. Moreover, since the disturbances caused by the eagles are not easy to quantify, we investigate the (indirect) correlation between the number of tourists and the number of eggs successfully hatched; this correlation can be determined from the data that Dr. Hentati-Sundberg kindly shared with our group.

A. Assumptions. Here we summarize the assumptions that we made when producing our model:

- Eagles are sensitive to human presence;
- Eagles do not directly harm/attack the murres;
- There are no major population disturbances other than the eagles (no diseases, etc.);
- All murres return to their nests after a disturbance (there is negligible immigration/emigration rate);
- Murres have access to all basic resources needed for survival (there is no shortage of food, water, etc.);
- All adult murres find a mate as long as there are enough adult murres present;
- All adult murres attempt to breed every season;
- A murre takes five years to reach adulthood and an additional two years to be able to successfully lay an egg;
- The relationship between the number of tourists and hatching and breeding success rates is linear;
- Island has a carrying capacity; having too many visitors breaks the model (c.f., Eqs [1b]-[1c]); [†]
- There is an equal number of male and female murres; this assumption is necessary to quantify the number of mating pairs, $M(t)$ (c.f., [1e]).
- Visitors return to the island linearly over time once Covid ends.

1. The Model

Consider the following equation describing the number of surviving eggs (N) as a function of time (t) and visitors (V):

$$N(t, V) = \lfloor [1 - d(V)]\, r(V) M(t) \rfloor . \qquad [1a]$$

Here, t is taken to be in years and $V(t)$ denotes the (time-dependent) number of visitors to the reserve. Moreover, $M(t)$ is a (time-dependent) function of breeding pairs, and $r(V)$ and $d(V)$ are the reproductive rate and death rate, respectively, of the murres (both quantities depend on the number of visitors, per our discussion on the Introduction). The floor

[*]We remark that similar disturbances have been observed by bald eagles (*Haliaeetus leucocephalus*) in North America. So the problem for the murres explained here is not specific to the white-tailed eagles [Parrish (1995)]

[†]This is a somewhat safe assumption, since the number of visitors required ro break the model (i.e., to make $d(V)$ nonpositive) is too high to be considered realistic. (Refer to Eq. [1c].)

function $\lfloor \cdot \rfloor$ allows for an integer number of eggs. By fitting reproduction and tourism data provided by Dr. Jonas Hentati-Sundberg depicted in Table 1, we can calculate both the reproductive rate (breeding success) and death rate (hatching failure) of newborn eggs as a function of the number of tourists:

$$r(V) = (7.8337 \times 10^{-5})V + 0.3201; \tag{1b}$$

$$d(V) = (-4.6068 \times 10^{-5})V + 0.3068. \tag{1c}$$

These relations showcase the overall positive effect of the presence of tourists on the eggs' hatching success, as was expected. In typical past years, the average number of tourists that visited the reserve during the murres' breeding season was between 4000 and 5000 individuals. In 2020, however, this number dropped to just 367 individuals. This is summarized in the following table:

Year	Breeding Success Rate	Hatching Failure Rate	Tourists
2017	0.673684211	0.101695	4642
2018	0.652631579	0.125	4279
2019	0.69047619	0.073171	4566
2020	Not available	0.288965	367

Table 1: Data provided by Dr. Jonas Hentati-Sundberg via personal correspondence

Lastly, we discuss $M(t)$, which denotes the number of adult breeding pairs capable of producing a successful egg. This quantity is calculated each year by adding the number of hatched chicks from seven years prior to the current amount of adult murres, and then dividing by two. We specifically chose 7 years based on the fact that the murres are not successful in breeding for the first 5-7 years of their lives, thus 7 was chosen to be the more pessimistic value. The adult population at time t, $A(t)$, is calculated as

$$A(t) = A(t-1) + N(t-7), \tag{1d}$$

which is then incorporated into the final count of breeding pairs

$$M(t) = \left\lfloor \frac{A(t)}{2} \right\rfloor. \tag{1e}$$

This function assumes that, at least for one breeding season, murres are monogamous; however they are allowed to choose the same or different partner every season. Lastly, we remark that the $N(t-7)$ term in Eq. [1d] makes the problem nonlinear.

Now, putting everything together, we can calculate the total population of murres at the end of a breeding season:

$$\boxed{P(t) = P(t-1) + N(t) - L(t)} \tag{2a}$$

where $N(t)$ comes from the calculations in Eqs. [1] and $L(t)$ is the number of murres that die in a year. The latter term takes into consideration that adult and young murres have different survival rates: Adults are considered to be ≥ 7 years of age, and they have a fixed adult survival rate which we denote by $\ell_{\geq 7}$. Young murres, on the other hand, have varying survival rates that depend on their age ($1 \leq t \leq 6$); we denote the respective survival rate by ℓ_i, with $i = t$ years old.[‡] Hence, we end up with the following expression for the number of murres' deaths in a year:

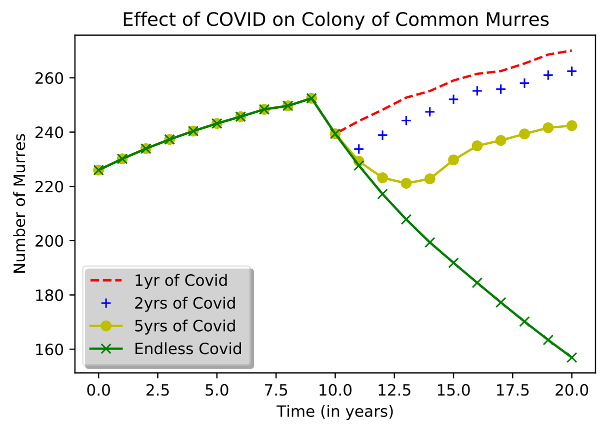
$$L(t) = \ell_{\geq 7} A(t) + \sum_{i=1}^{6} \ell_i Y_i(t), \tag{2b}$$

where $Y_i(t)$ is the population of young murres of age i in year t; this quantity is related to the number of surviving eggs per the expression

$$Y_i(t) = N(t-i) \quad i = 1, \ldots, 6. \tag{2c}$$

2. Results & Conclusions

A simulation of the model presented on Eqs. [1]– [2] is ran over the course of twenty years (2017–2037). The following plot shows what would happen to the colony of murres at Stora Karlsö if Covid restrictions remained in place; we consider scenarios with varying degrees of optimism, from the most hopeful case (Covid ends in just one year) to the most pessimistic situation where restrictions are not lifted at all for the next twenty years. The tangible (if indirect) impact of the lack of tourists on the colony of murres is evident.



As the figure indicates, if Covid restrictions are lifted over the next few years, the murres population of the colony should be able to recover. That being said, we note that, while in the cases of 1-year and 2-years of Covid the population recovers at an equally impressive rate, the 5-year scenario shows that recovery would be much slower if Covid restrictions linger a bit longer.

On the other side of the spectrum, in the most pessimistic scenario where restrictions remain imposed indefinitely, we see the detrimental effect that it could have on the colony. Note also that for most of the first decade all four scenarios are identical; this is to be expected since the disturbances are affecting the number of eggs succesfully hatching, not the young or adult murres directly. Thus the effect of the disturbances on the murres' population is not immediately obvious.

Lastly, we remark that the model does not take into account a logistic component; in the absence of the disturbances caused by the Covid restrictions the murres' population would continue to grow endlessly. While this is not realistic, we considered logistic growth to be irrelevant for our investigations, since our focus is entirely on the Covid-related disturbances.

Appendix A: Simulation Code

For completeness, we present in this appendix the Python script that implements our model:

```
import numpy as np
import matplotlib.pyplot as plt

# In the simulation we allow non-integer values of
    birds and eggs
font = {'family' : 'serif',
        'weight' : 'normal',
        'size'   : 14}
```

[‡] All survival rate data was acquired from [Sarzo et al. (2019)].

```

#survival rates
# taken from Bayesian Immature survival ... by Sarzo Blanca et al. published in The Waterbird Society
asr = 0.905574
y1r = 0.53
y2r = 0.87
y3r = 0.96


# egg deaths as function of tourists (D(V))
def death_per_tourists(num_tourists) :
    return num_tourists*(-4.6068*(10**(-5))) + 0.3068


# reproductive rate (r(V))
def repro_rate_tourists(num_tourists):
    return num_tourists*(7.8337*(10**(-5))) + 0.3201

# number of maiting pairs over time
number = 250;
adult_murres_over_time_new1 = [np.floor(number*asr)];
adult_murres_over_time_new2 = [np.floor(number*asr)];
adult_murres_over_time_new5 = [np.floor(number*asr)];
adult_murres_over_time_new17 = [np.floor(number*asr)];

# number of tourists in different Covid scenarios
tourists_per_year1 = [
                     4642,4279,4566,367,4642,4566,
                     4642,4279,4566,4642,4279,4566,
                     4642,4279,4566,4642,4279,4566,
                     4642,4279
                     ];
tourists_per_year2 = [
                     4642,4279,4566,367,(4642-367)/2,
                     4566,4642,4279,4566,4642,4279,
                     4566,4642,4279,4566,4642,4279,
                     4566,4642,4279
                     ];
tourists_per_year5 = [
                     4642,4279,4566,367,(4642-367)/5,
                     2*(4642-367)/5,3*(4642-367)/5,
                     4*(4642-367)/5,4566,4642,4279,
                     4566,4642,4279,4566,4642,4279,
                     4566,4642,4279
                     ];
tourists_per_year17 = [
                      4642,4279,4566,367,367,367,367,
                      367,367,367,367,367,367,367,367,
                      367,367,367,367,367
                      ];

#initializing
val = tourists_per_year1[0];

temp_val = (
            repro_rate_tourists(val)
            - repro_rate_tourists(val)
            * death_per_tourists(val)
            ) * (number/2);

# array = [eggs,1yr old, 2 yrs old, ... 6 yrs old]
young_murres_over_time = [
                        temp_val,
                        temp_val*y1r,
                        temp_val*y1r*y2r,
                        temp_val*y1r*y2r*y3r,
                        temp_val*y1r*y2r*y3r*asr,
                        temp_val*y1r*y2r*y3r*(asr**2)
                        ];

surival_rate_array = [1,y1r,y2r,y3r,asr,asr];


# Covid lasts 1 year
for val in tourists_per_year1:
    # add latest value in young array to adult first
    adult_murres_over_time_new1.append(
            adult_murres_over_time_new1[-1]
            + young_murres_over_time[-1]
            );

    num_mating_pairs =
        np.floor((adult_murres_over_time_new1[-1])/2);

    # shift values in young array
    young_murres_over_time =
        np.roll(young_murres_over_time,1);

    num_eggs =
        (
          repro_rate_tourists(val)
        - repro_rate_tourists(val)
         *death_per_tourists(val)
        )
         *num_mating_pairs;

    # break out into
    adult_murres_over_time_new1[-1] *= asr;
    young_murres_over_time[0] = num_eggs;
    young_murres_over_time =
        np.multiply(
            young_murres_over_time,
            surival_rate_array
            );


# re-initialize
young_murres_over_time = [
                        temp_val,
                        temp_val*y1r,
                        temp_val*y1r*y2r,
                        temp_val*y1r*y2r*y3r,
                        temp_val*y1r*y2r*y3r*asr,
                        temp_val*y1r*y2r*y3r*(asr**2)
                        ];


# Covid lasts 2 year
for val in tourists_per_year2:
    adult_murres_over_time_new2.append(
            adult_murres_over_time_new2[-1]
            + young_murres_over_time[-1]
            );

    num_mating_pairs =
        np.floor((adult_murres_over_time_new2[-1])/2);

    # shift values in young array
    young_murres_over_time =
        np.roll(young_murres_over_time,1);

    num_eggs =
        (
          repro_rate_tourists(val)
        - repro_rate_tourists(val)
         *death_per_tourists(val)
        )
         *num_mating_pairs;

    # break out into
    adult_murres_over_time_new2[-1] *= asr;
    young_murres_over_time[0] = num_eggs;
    young_murres_over_time =
        np.multiply(
            young_murres_over_time,
            surival_rate_array
            );


# re-initialize
young_murres_over_time = [
                        temp_val,
                        temp_val*y1r,
                        temp_val*y1r*y2r,
                        temp_val*y1r*y2r*y3r,
                        temp_val*y1r*y2r*y3r*asr,
                        temp_val*y1r*y2r*y3r*(asr**2)
                        ];



# Covid lasts 5 year
for val in tourists_per_year5:
    adult_murres_over_time_new5.append(
            adult_murres_over_time_new5[-1]
            + young_murres_over_time[-1]
            );
```

```
    num_mating_pairs =
        np.floor((adult_murres_over_time_new5[-1])/2);

    # shift values in young array
    young_murres_over_time =
        np.roll(young_murres_over_time,1);

    num_eggs =
        (
          repro_rate_tourists(val)
        - repro_rate_tourists(val)
         *death_per_tourists(val)
        )
         *num_mating_pairs;

    # break out into
    adult_murres_over_time_new5[-1] *= asr;
    young_murres_over_time[0] = num_eggs;
    young_murres_over_time =
        np.multiply(
            young_murres_over_time,
            surival_rate_array
            );


# re-initialize
young_murres_over_time = [
                         temp_val,
                         temp_val*y1r,
                         temp_val*y1r*y2r,
                         temp_val*y1r*y2r*y3r,
                         temp_val*y1r*y2r*y3r*asr,
                         temp_val*y1r*y2r*y3r*(asr**2)
                         ];

# Covid lasts 17 years
for val in tourists_per_year17:
    adult_murres_over_time_new17.append(
            adult_murres_over_time_new1[-1]
            + young_murres_over_time[-1]
            );

    num_mating_pairs =
        np.floor((adult_murres_over_time_new1[-1])/2);

    # shift values in young array
    young_murres_over_time =
        np.roll(young_murres_over_time,1);

    num_eggs =
        (
          repro_rate_tourists(val)
        - repro_rate_tourists(val)
         *death_per_tourists(val)
        )
         *num_mating_pairs;

    # break out into
    adult_murres_over_time_new17[-1] *= asr;
    young_murres_over_time[0] = num_eggs;
    young_murres_over_time =
        np.multiply(
            young_murres_over_time,
            surival_rate_array
            );

time = np.arange(len(adult_murres_over_time_new1));

# Create the figure and axes
fig, ax1 = plt.subplots(1, 1)


# Add labels for the legend
function1 = ax1.plot(
                     time, adult_murres_over_time_new1,
                     'r--', label=r'1yr of Covid'
                    );
function2 = ax1.plot(
                     time, adult_murres_over_time_new2,
                     'b+', label=r'2yrs of Covid'
                    );


function3 = ax1.plot(
                     time, adult_murres_over_time_new5,
                     'y-o', label=r'5yrs of Covid'
                     );
function4 = ax1.plot(
                     time, adult_murres_over_time_new17
    ,
                     'g-x', label=r'Endless Covid'
                     );

# Create the legend by first fetching the labels from
    the functions
functions = function1 + function2
          + function3 + function4
labels = [f.get_label() for f in functions]
plt.legend(
           functions,labels,fancybox=True,
           framealpha=0.5,borderpad=0.5,
           shadow=True,loc=0
          )

# Add labels and title
ax1.set_xlabel(r'Time (in years)')
ax1.set_ylabel(r'Number of Murres')
plt.title('Effect of COVID on Colony of Common Murres')

# plt.show()
# Save the figure
plt.savefig(
            '../Figures/Murres.pdf',
            bbox_inches='tight'
           )
plt.close()
```

Appendix B: The Leslie Matrix Model

An alternative model that could also be considered is the so-called *cohort population model* (also known as the *Leslie matrix model*). It is a discrete model particularly useful in studying the dynamics in populations where the level of reproductive activity is nonuniform over a normal lifetime. [Luenberger (1979)] In this model the murres' population is divided into age groups (or *cohorts*) of equal age span (we choose one year for the age span). That is, the first group consists of all those members of the population between the ages of zero and one year (this would include the newly hatched eggs of that year), the second consists of those between one and two, and so on.

Now let $M_i(k)$ be the population of murres of the i^{th} age group at time period k (the groups are indexed sequentially from 0 through n). Then to describe the system's behavior, it is only necessary to describe how these numbers change during one time period. Aside from the possibility of death, it is clear that during one time period the cohorts in the i^{th} age group simply move up to the $(i+1)^{th}$ age group . To account for the death rate of individuals within a given age group, the upward progression is attenuated by a survival factor. [Luenberger (1979)] The net progression can be described by the simple equations

$$M_{i+1}(k+1) = S_i M_i(k) \quad i = 0, 1, \dots, 7,$$

where S_i is the survival rate of the i^{th} age group during one period. The only age group not determined by the equation above is $M_0(k+1)$, the group of individuals born during the $(k+1)$-time period (hatched eggs). The number in this group depends on the ratio (hatched eggs over laid eggs) of each age group (and this ratio depends on the number of visitors (V), as seen in Eq. [1]):

$$M_0(k+1) = \sum_{i=0}^{7} r_i M_i(k),$$

where, r_i are the ratio (hatched eggs over laid eggs) of each age groups.

Clearly, $r_i = 0$ for $0 \leq i \leq 6$; however, for $i > 6$, we have nonzero ratios $r_i(V)$. In summary, the model has the form

$$\begin{pmatrix} M_0(k+1) \\ M_1(k+1) \\ \cdot \\ \cdot \\ \cdot \\ M_n(k+1) \end{pmatrix} = \begin{pmatrix} r_0 & r_1 & r_2 & . & . & . & r_n \\ S_0 & 0 & 0 & 0 & . & . & 0 \\ . & . & . & . & . & . & . \\ . & . & . & . & . & . & . \\ . & . & . & . & . & . & . \\ 0 & 0 & 0 & 0 & . & . & S_n \end{pmatrix} \begin{pmatrix} M_0(k) \\ M_1(k) \\ \cdot \\ \cdot \\ \cdot \\ M_n(k) \end{pmatrix}.$$

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