Supplementary Information for 'Deciding when to intrude on a neighbour: Quantifying behavioural mechanisms for temporary territory expansion'

Supplementary Appendix A

The justification for Equation (2) from the Main Text uses a resource depletion-and-renewal argument. Consider an otter group with N individuals in a territory of length M. Although M may vary over time, we assume that the resource distribution across the territory equilibriates in a much shorter time than the time between successive changes in territory size. Thus the resource distribution can be assumed to be fixed for the purposes of this appendix.

During a time interval, τ, the resources $R(x,t)$ at each point x change with the following dynamics

$$R(x,t+\tau) = \begin{cases} [1-d(N)]R(x,t), & \text{if the group is at } x \text{ between times } t \text{ and } t+\tau, \\ R(x,t) + rR(x,t)\left(1-\frac{R(x,t)}{K}\right), & \text{otherwise,} \end{cases} \tag{1}$$

where $d(N) > 0$ and $0 < r < 1$ to avoid oscillatory or chaotic resource dynamics. Note that this is a discrete-time model, so the values of $d(N)$ and r implicitly depend upon τ. Assuming that the location of the group and direction of movement is picked uniformly at random, the probability of the group passing through an arbitrary point x between times t and $t+\tau$ can be estimated to be l/M.

Because resources (fish) and their environment (rivers) are highly mobile, we assume that the resources rapidly settle to a mean value across the territory. The dynamics of the mean

resources, $\bar{R}(t)$, are then given by

$$\bar{R}(t+\tau) = \frac{l[1-d(N)]\bar{R}(t)}{M} + \frac{M-l}{M}\left[\bar{R}(t) + r\bar{R}(t)\left(1-\frac{\bar{R}(t)}{K}\right)\right]. \tag{2}$$

The steady-states $\bar{R} = \lim_{t\to\infty}\bar{R}(t)$ are then given by replacing $\bar{R}(t)$ and $\bar{R}(t+\tau)$ by $\bar{R}$ in Equation (2) and solving to give $\bar{R} = 0$ or

$$\bar{R} = K\left[1 - \frac{d(N)}{r}\frac{l}{M-l}\right]. \tag{3}$$

Since $0 < r < 1$, the latter is the unique stable steady state, as long as the right-hand side of Equation (3) is positive (this follows from well-known properties of the discrete logistic map - see e.g. May (1976)). Furthermore, $R(t)$ tends to $K\left[1 - \frac{d(N)}{r}\frac{l}{M-l}\right]$ as $t \to \infty$ whenever $R(0) > 0$. If the right-hand side of Equation (3) is negative, $R(t)$ decreases whenever it is positive, so $R(t) \to 0$ as $t \to \infty$. Hence we arrive at Equation (2) from the Main Text.

Supplementary Appendix B

Here, we derive the equation for energetic gain, E_G, given as Equation (3) in the Main Text. We begin by calculating P_L, the probability that the otter group is Scenting at a randomly selected point in time. Let $T_F(x)$ be the mean first passage time from $x \in [0, L_1]$ to L_1 of the otter group in Scenting state. Let $\bar{T}_F$ be the average of $T_F(x)$ over all possible starting points $x \in [0, L_1]$. Then $\bar{T}_F$ is the mean time spent on a Scenting trip. Now, the time between consecutive Scenting trips is $t_L(N_1)$. Therefore

$$P_L = \frac{\bar{T}_F}{t_L(N_1) + \bar{T}_F}. \tag{4}$$

Furthermore, $\bar{T}_F$ can be calculated as follows

$$\bar{T}_F = \frac{\tau}{lL_1} \int_0^{L_1} (L_1 - s)\mathrm{d}s = \frac{\tau L_1}{2l}, \tag{5}$$

so that

$$P_L = \frac{L_1 \tau}{2l t_L(N_1) + L_1 \tau}. \tag{6}$$

Now, as long as the energy level is sufficiently lower than $E_{\max}$, we can derive from Equation (6) the average energy gained by an individual per time-step τ. For this, we start by noting that Equation (1) and (2) from the Main Text imply that the energetic gains when Foraging and when Scenting are, respectively,

$$\begin{aligned} E_G^F &= alK \left[1 - \frac{d(N_1)}{r} \frac{l}{L_1 - l}\right] - E_\tau, \\ E_G^S &= \gamma alK \left[1 - \frac{d(N_1)}{r} \frac{l}{L_1 - l}\right] - E_\tau. \end{aligned} \tag{7}$$

Then the average energetic gains per time-step are given by $E_G = P_L E_G^S + (1 - P_L) E_G^F$ so that, after some algebraic manipulation,

$$E_G = \frac{alK}{2lt_L(N_1) + L_1\tau} \left(1 - \frac{d(N_1)}{r} \frac{l}{L_1 - l}\right) [\gamma\tau L_1 + 2lt_L(N_1)] - E_\tau. \tag{8}$$

The expression for E_G has several redundant parameters, so we introduce the following composite parameters

$$\Lambda_1 = \frac{L_1}{l}, \quad \alpha = aKl, \quad D(N_1) = \frac{d(N_1)}{r}, \quad T_L(N_1) = \frac{t_L(N_1)}{\tau}. \tag{9}$$

This gives the following expression for the energy gain per time-step

$$E_G = \frac{\alpha}{2T_L(N_1) + \Lambda_1} \left(1 - \frac{D(N_1)}{\Lambda_1 - 1}\right) [\gamma\Lambda_1 + 2T_L(N_1)] - E_\tau. \tag{10}$$

This is Equation (3) from the Main Text.

Supplementary Appendix C

In this section, we derive Equation (6) from the Main Text. During the period of time t_C after a call, the energy of Group 1 has the following dynamics

$$E_1(t+\tau) = \min\{N_1 E_{\max}, E_1(t) + N_1(al\bar{R}_1(t) - E_\tau)\}, \tag{11}$$

where

$$\bar{R}_1(t) = K\left[1 - \frac{d(N_1)}{r}\frac{l}{C_1 - l}\right]. \tag{12}$$

Making a call also incurs a penalty due to the fact that otters uptake less energy from the environment when making a Calling trip than they do when Foraging (this is encoded in the parameter γ - see Table 1 from the Main Text). The mean time from an arbitrary point x in $[0, L_1]$ (chosen uniformly at random) to the calling point C_1 is given by

$$\bar{T}_F = \frac{\tau(2C_1 - L_1)}{2l}. \tag{13}$$

As the group makes a Calling trip, there is a chance that they will encounter Group 2 and have an aggressive interaction. This would incur a loss of energy of $\mu E_{\max}$ (implicitly, we assume that a maximum of one interaction occurs in this short time interval). Assuming that the position distribution of Group 2 is uniform across $[L_2, L]$, the probability of an interaction happening is estimated as

$$\frac{C_1 - L_2}{L - L_2}. \tag{14}$$

Hence the expected energetic loss, per individual, due to interactions, in a single Calling trip is

$$\frac{C_1 - L_2}{L - L_2}\mu E_{\max}. \tag{15}$$

Overall, the expected energetic loss of each individual during a Calling trip is

$$\frac{C_1 - L_2}{L - L_2}\mu E_{\max} - \frac{2C_1 - L_1}{2l}\left[\gamma alK\left(1 - \frac{d(N_1)}{r}\frac{l}{L_1 - l}\right) - E_\tau\right]. \tag{16}$$

Having computed the energetic cost of making a Calling trip, we now calculate the gain enjoyed by the enlargened territory after the call is made. From Equations (11-12), the expected energetic gain per individual, in the period of time t_C after the call is made (assuming that $E_{\max}$ is never reached), can be calculated as

$$\frac{t_C}{\tau}\left\{Kal\left[1 - \frac{d(N_1)}{r}\frac{l}{C_1 - l}\right] - E_\tau\right\}. \tag{17}$$

By subtracting Equation (16) from Equation (17), we obtain the estimated energetic gain per individual for the whole period from deciding to make a call to the time when the calling cue is no longer active to be

$$\begin{aligned} E_G^C =& \frac{t_C}{\tau}\left\{Kal\left[1 - \frac{d(N_1)}{r}\frac{l}{C_1 - l}\right] - E_\tau\right\} - \\ & \frac{C_1 - L_2}{L - L_2}\mu E_{\max} + \frac{2C_1 - L_1}{2l}\left[\gamma\alpha lK\left(1 - \frac{d(N_1)}{r}\frac{l}{L_1 - 1}\right) - E_\tau\right]. \end{aligned} \tag{18}$$

In the case $\gamma = 0$, and using the composite parameters defined in Equation (9), we have

$$E_G^C(\gamma = 0) = T_C\alpha\left[1 - \frac{D(N_1)}{\Gamma_1 - 1}\right] - E_\tau\left[T_C + \frac{2\Gamma_1 - \Lambda_1}{2}\right] - \frac{\Gamma_1 - \Lambda_2}{\Lambda - \Lambda_2}\mu E_{\max}. \tag{19}$$

where, in addition to Equation (9), we have introduced the parameters $T_C = t_C/\tau$, $\Gamma_i = C_i/l$, $\Lambda_2 = L_2/l$, and $\Lambda = L/l$.

Thus, if the energetic gain given by Equation (19) is larger than the expected energetic gain for the same period of time using a pure-Scenting strategy (see Equation 5 from the Main Text), then there is some benefit to the animal for employing a Calling strategy. The inequality that needs to be satisfied for such a benefit to apply is

$$E_G^C > E_G \left[T_C + \frac{2\Gamma_1 - \Lambda_1}{2} \right]. \tag{20}$$

In the case $\gamma = 0$, this is equivalent to the following inequality, which is Equation (6) from the Main Text

$$\begin{aligned} T_C \left[\alpha \left(1 - \frac{D(N_1)}{\Gamma_1 - 1} \right) - \frac{2\alpha T_L(N_1)}{2T_L(N_1) + \Lambda_1} \left(1 - \frac{D(N_1)}{\Lambda_1 - 1} \right) \right] > \\ \mu E_{\max} \frac{\Gamma_1 - \Lambda_2}{\Lambda - \Lambda_2} + \frac{2\Gamma_1 - \Lambda_1}{2} \left(1 - \frac{D(N_1)}{\Lambda_1 - 1} \right) \frac{2\alpha T_L(N_1)}{2T_L(N_1) + \Lambda_1}. \end{aligned} \tag{21}$$

Supplementary Appendix D

To assess the effect of a non-constant resource distribution across each territory, we consider two different scenarios. In Scenario A, the resources are concentrated towards the centre of each territory (i.e. points 0 and L). In Scenario B, they are concentrated towards the border between the two territories (i.e. the point $L_1 = L_2 = L/2$).

Specifically, we replace the value of $\bar{R}_i(t)$ from Equation (2) with the following piecewise-linear expression

$$\bar{R}_i(x,t) = \max\left\{0, K\left[1 - \frac{d(N_i)}{r}\frac{l}{M_i(t)-l}\right] - \frac{Ls}{4} + \left|\frac{L}{2} - x\right| s\right\}, \tag{22}$$

which now depends on the position, x, of the group. We have also introduced the constant s into Equation (22), which denotes the slope of the resources away from the central point, $L/2$. Scenario A requires a positive value of s, which we pick as $s = K/40$. Scenario B requires a negative value of s, which we pick as $s = -K/40$.

If resources are non-constant throughout the territory, it makes sense to assume that otters will bias their movement up the resource gradient. Therefore, whilst Foraging, instead of having an equal chance of moving left or right, we assume that the probability of moving up the resource gradient is $p = \exp(s)/[1+\exp(s)]$ and the probability of moving down the gradient is $1-p$. Notice that when $s = 0$, we have $p = 1/2$, whilst $\lim_{s\to\infty}(p) = 1$ and $\lim_{s\to-\infty}(p) = 0$.

Other than these changes, we use the same parameters as in the Section 'Calling and Scenting' from the Main Text: $\delta = 0.4, \epsilon = 20, E_\tau = 15, \alpha = 40, L_1 = 5, L_2 = 5, L = 10, E_{\max} = 500, \mu = 0$. Similarly to the 'Calling and Scenting' Section, we assume that Group 2 can survive in perpetuity without Calling. Therefore we can compare the results here directly with those from the 'Calling and Scenting' Section.

Results are summarised in Fig. S1. As in the case of constant resources (see Fig. 4 from the Main Text), Calling can improve the chances of survival by a large amount, especially when the Calling site is chosen well into the other group's territory. However, the extent of the

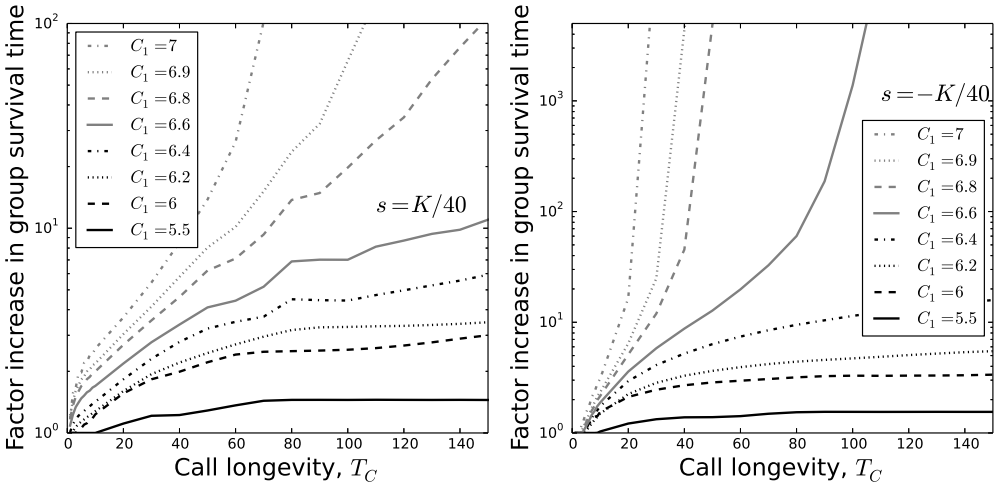

Fig. S1. The effect of non-constant resources. To be compared with the middle panel of Fig. 4 from the Main Text, where resources are constant across each territory. The left-hand panel (resp. right-hand panel) displays 'Scenario A' (resp. Scenario B), where resources are concentrated towards the centre of each territory (resp. border between two territories). Note different scales on the vertical axes of the two panels.

improvement is much more pronounced in Scenario B but slightly less pronounced in Scenario A. This makes intuitive sense, as in Scenario B there is much more resource near the territory border, so there is more value in securing that resource temporarily by Calling.

Supplementary Appendix E

To test the sensitivity of our parameter choices on the conclusions we make in the 'Calling and Scenting' Section of the Main Text, we vary each of the parameters $\delta, \epsilon, E_\tau = 15, \alpha, E_{\max}, \mu$, one-at-a-time, and re-run the simulations required to produce a plot of "Maximum factor increase in co-existence time" (see Fig. 5 in the Main Text), for each new set of parameter values. For each of $\delta, \epsilon, E_\tau = 15, \alpha, E_{\max}$, we increase the parameter value by 10%. Since $\mu = 0$ in the Main Text, we increase this to $\mu = 0.1$ for our sensitivity analysis. Results are displayed in Fig. S3. We observe that, for each set of parameter values, the overall story is the same, of a non-monotonic relationship between co-existence time and calling point, with the maximum occuring somewhere around $C_1 = 6.5$. This suggests that the central messages of the simulation analysis are robust to small changes in parameter values.

References

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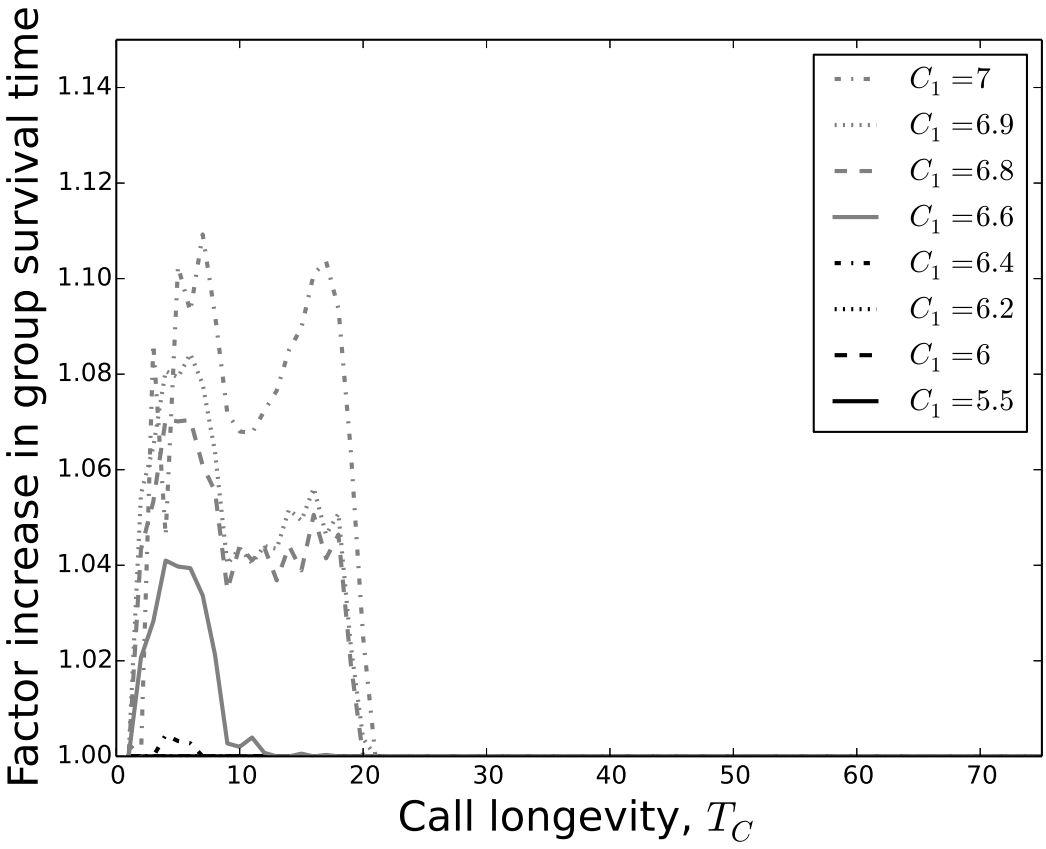

Fig. S2. Little-to-no benefit of Calling when both groups cannot survive on a pure-Scenting strategy. Here, $N_1 = N_2 = 9$ and other parameters are as in the 'Calling competition' Section from the Main Text. For all values of T_C and C_1, Calling only increases the co-existence time very little, if at all. Interestingly, the increase factor in co-existence time decays as T_C becomes large, which is the opposite effect to that seen in Fig. 4 of the Main Text. A higher T_C means that after a Call, one group is forced into a smaller territory for a longer period of time. During this time, there is a higher chance that this group's energy reaches zero. When the competition is asymmetric, so that one group is more resilient to smaller territories (as in cases with groups of different sizes, Figs. 4 and 5 of the Main Text) this effect is much less likely to be observed.

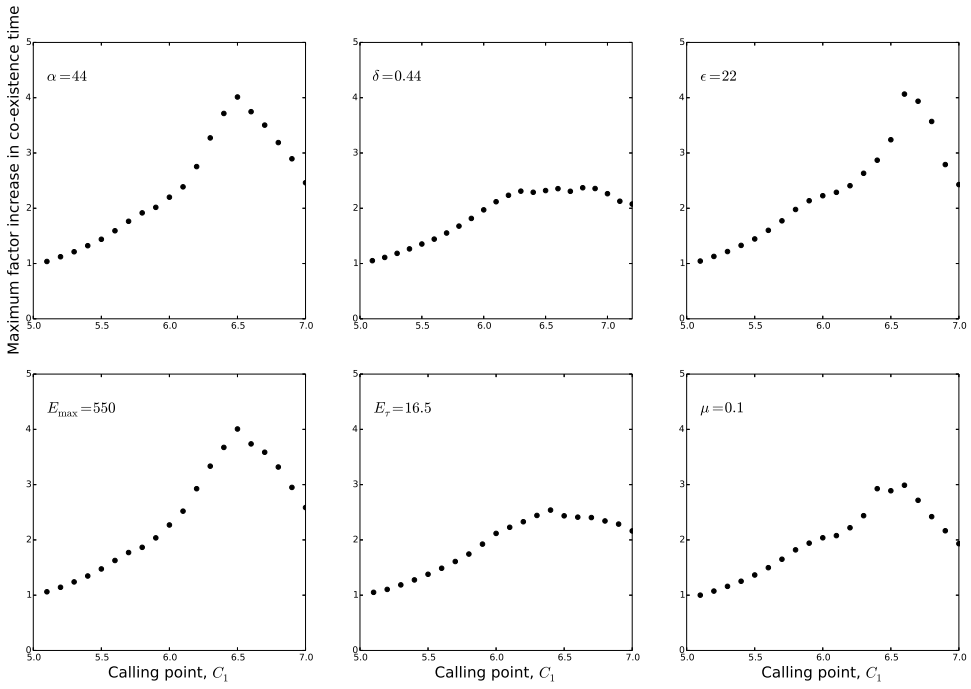

Fig. S3. Sensitivity analysis. Output of simulations as described in the 'Calling and Scenting' Section of the Main Text, with small changes in input parameters. Unless otherwise stated in the panel, the parameter values used for the simulations are as stated in the Main Text, namely $\delta = 0.4, \epsilon = 20, E_\tau = 15, \alpha = 40, E_{\max} = 500, \mu = 0$.