The energy cost of singing in wild rock hyrax males: evidence for an index signal

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In many species individuals advertise their quality via vocal communication. Although sound production requires energy, it is still unclear to what extent vocalizing increases metabolic rate. A substantial energetic cost of vocalization may suggest that it serves as a handicap. In this study, we evaluated the energetic cost of vocalization in the context of other activities in a free-living mammal. In the rock hyrax, Procavia capensis, males produce loud complex songs that convey multiple types of information about the singer. We used the doubly labelled water method to estimate field metabolic rate (FMR), in males that were collar-fitted with miniaturized recorders. Higher-ranked males sang longer songs, which also featured higher sound energy. However, contrary to our predictions, the duration of singing was negatively correlated with FMR, whereas the duration of other social sounds, typically associated with social conflicts, had a positive effect on FMR. We suggest that higher-ranking males expend overall less energy due to lower intrinsic metabolism, and thus the singing duration effect on FMR is a reflection of social rank. Rock hyrax singing is therefore assessed as requiring a high effort over a short period but not as a lengthy activity, matching the category of index signals. Singing may also serve as a handicap to the signaler, not because of its energetic cost but because it exposes the singer to potential predation. Our study is the first to record the activities and vocalizations of a free-living mammal in such detail. We discuss the costs and benefits of hyrax songs, suggesting that singing males trade safety from predators for increasing their reputation.

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Vocalizations may also be costly in other ways, not related to energy costs. They may attract predators, require time that could be spent in other activities, and require learning and specialization of brain areas (Gil & Gahr 2002). Therefore, vocalizing individuals may be advertising their quality even if the energy cost of the signal itself is not high.

The rock hyrax, Procavia capensis, is a social mammal that lives in mixed-sex groups, consisting in our study area of several males (one mature immigrant resident and several natal late dispersers) and 5–20 females with their pups (Koren et al. 2006; Ilay et al. 2011). Females constitute the core of the group, while resident males remain with a group for up to 4 years (Koren et al. 2006). Breeding is seasonal and synchronized (Neaves 1973), and females mate with multiple males, masking paternity (Koren & Geffen 2009). Adolescent males (i.e. 17–24 months old) are forced to disperse (Hoeck et al. 1982) and they live on the periphery of colonies (Koren et al. 2008).

Acoustic communication constitutes the most widely used means of information transfer among rock hyraxes (Fourie 1977). Adult male hyraxes engage throughout most of the year in rich and complex vocalization behaviour that we term ‘singing’ (Koren et al. 2008). Singing in the rock hyrax may be related to sexual advertisement since it abruptly decreases for a few months following the mating period (Koren et al. 2008). Rock hyrax male songs are complex signals that encode multiple types of information, such as identity, age, mass, size, social rank and hormonal status of the singer (Koren & Geffen 2009, 2011). Males sing in different contexts, such as after winning an agonistic interaction with another male, or in response to singing by other males (Ilay et al. 2011). Hyraxes also produce other types of vocalization, such as twitters that are used in short-range communication, and grunts, howls and clicks, used in agonistic interactions.

In this study we sought to determine whether singing constitutes a significant part of the time budget and, consequently, affects the energy expenditure of males, and could thus serve as a handicap. Alternatively, if singing does not serve as a handicap, it may be an index signal, which can convey information about the singer without exhausting weaker individuals (Clark 2012). We formulated the following two sets of hypotheses and predictions to test the role of singing and how it relates to male quality.

(1) We hypothesized that singing duration and amplitude can serve as a handicap. Under this scenario, high-quality males are predicted to obtain higher social status and to sing longer and louder songs, relative to lower-quality males. Thus, high-quality males are expected to expend more energy. Furthermore, this substantial increase in the cost of singing may also negatively affect longevity of high-quality males.

(2) Alternatively, we hypothesized that singing can serve as an index signal. Singing is not predicted to cause an increase in energy expenditure. Other factors, such as foraging activities or social interactions, may be responsible for the variance in energy expenditure. High-ranked males may still sing more than others, because singing serves as an indicator of male quality. Since singing is not energetically costly, high-ranked males should not suffer reduced longevity, unless singing increases predation risk.

In addition, we hypothesized that the more frequent singers engage less in costly social interactions (i.e. aggressive encounters). Since songs provide information about the singer, singing males may advertise their quality and thereby may reduce the need for such costly social interactions. Thus, while singing probably consumes more energy than resting, it may conserve energy when calculating the overall budget, by reducing other costly activities (Kunc & Wolf 2008). Furthermore, individual recognition based on acoustic signals is common among mammals (e.g. Vannoni & McElligott 2007), potentially facilitating advertisement via vocalization. If singing serves as an advertisement, then stronger males may convey their qualities to conspecifics, lowering the motivation of the listeners to fight them. Thus, we predicted a negative correlation between singing duration and the duration of social sounds produced in aggressive interactions.

To address these hypotheses, we fitted miniaturized digital recorders to male hyraxes, and in conjunction, determined the energy expenditure (field metabolic rate, FMR) of the same males using the doubly labelled water method. The recorders recorded all types of vocalizations, in addition to other activities such as moving and feeding, allowing us to calculate the duration of songs and their amplitude, as well as the duration of sounds used in social interactions. We also observed focal males in interactions with conspecifics and determined their social ranks.

METHODS

Ethical Note

The rock hyrax is a wild animal protected under Israeli law. The Nature and Parks Authority (NPA), the governmental agency responsible for nature conservation in Israel, issues all relevant research permits. Permits for capturing, marking and handling hyraxes in Ein Gedi were issued and reviewed annually by the NPA (permit numbers: 2007/27210, 2008/31138, 2009/32871, 2010/37520).

Study Site and Population

Fieldwork took place in two deep gorges, David and Arugot, in the Ein Gedi Nature Reserve (31°28′N, 35°24′E), Israel. In each gorge we monitored two to three mixed-sex groups and the bachelor males on their peripheries.

Live box traps (Tomahawk Live Trap Co, Tomahawk, WI, U.S.A.) were set before first light (approximately 90 min before dawn) with kohlrabi and cabbage as bait, and operated until late morning, with inspections every 2 h. Traps were placed in shaded locations and were not vulnerable to predators. No water was supplied in the traps as hyraxes are rarely observed drinking. Newly trapped animals were anaesthetized with ketamine hydrochloride (0.1 ml/kg intramuscular injection), weighed, measured, photographed and individually marked using small (1 cm) cylindrical subcutaneous glass transponders (DataMars SA, Bedano-Lugano, Switzerland) that were inserted into the neck region and remained there for life. For identification from a distance, we also fitted all adult individuals with a light numbered collar (<5 g). No adverse effects of the transponders or the collars were observed during the 12 years of study. All measurements were recorded in situ, and the animals were returned to the traps for full recovery (3 h), and thereafter released back at the capture site. All animals were handled and marked in shaded places to prevent heat shock. Animals resumed full normal activity following their release.

Behavioural Observations

Hyrax activity was observed daily during the field season (April–August) using 10×42 binoculars and a telescope with ×25–75 magnification (ED-82A spotting scope, Nikon, Japan). Observations were conducted in the morning from first light to noon, when hyraxes in Ein Gedi retreat to their shelters. Each day, one focal group, out of the five mixed-sex groups we regularly monitored, was randomly chosen and observed (Altmann 1974). One observer scanned the area using binoculars, locating individuals, while the other used a telescope to identify the animals from their markings. Using this method we were able to record multiple social
interactions within a group, including interactions of nongroup members in the same area. Agonistic behaviour was reflected in a combination of typical actions and postures, such as displaying the large incisors, growling, grinding molars, snapping, and chasing and biting others (Barocas et al. 2011). For each field season (2008–2010), we calculated the social rank of each male using the David’s score method (Gammell et al. 2003). When calculating the overall success of an individual, the David’s score takes into account the success of an individual’s rivals. Thus, individuals that won interactions with higher-ranked individuals received a higher score. In addition, we counted the number of singing events and aggression events for each male. These parameters were divided by the number of days that each male was observed to facilitate comparison with other males. Finally, to relate longevity to social status, we compared social status of all males of known age that died.

Field Metabolic Rate Measurements

Field metabolic rate of mature, free-living hyrax males was measured using the doubly labelled water method (DLW, $^{18}$H$^{2}$O; Lifson & McClintock 1966; Nagy 1980; Kam & Degen 1997; Speakman 1997), which facilitates estimation of CO$_2$ production over time. The advantage of the DLW method is that it provides a direct estimate of field metabolic rate that is independent of assumptions regarding the modes of energy utilized (Butler et al. 2004). The DLW method has been validated in many species and is currently the best method for estimating field metabolic rate (Nagy et al. 1999). This method depends on accurate injection of DLW and on an assumption about the type of diet (see below). In this study, we followed the analytical method suggested by Nagy (1980), which indicates accuracy to within 3%. During the summers of 2008–2010, we chose 10 focal males that had demonstrated a high recapture rate, to ensure that we could trap them within 10 days. Captured individuals were weighed to the nearest 10 g and injected intraperitoneally (using a gastight syringe; Hamilton, Reno, NV, U.S.A.) with 1.50 ml of DLW containing 97% atoms of $^{18}$O (Rotem Industries, Beer Sheva, Israel) and 3.7 MBq of tritium per ml (New England Nuclear, Boston, MA, U.S.A.). We allowed 4 h for equilibration of the isotopes with body fluids (Degen et al. 1997), during which time neither food nor drinking water were available (the waiting time occurred around noon, at a time when hyraxes usually rest in a shady place), then we collected a blood sample (about 1 ml) from the cephalic vein. The animals were then fitted with a miniaturized recorder (detailed below) and released back at the point of capture. Animals were recaptured 4–8 days later, and a second blood sample was collected. They were then weighed and released.

Blood samples were microdistilled (Nagy 1983) and analysed for $^{18}$O concentration (atom %) and $^3$H levels (at Metabolic Solutions Inc., Nashua, NH, U.S.A.). Total body water volume was estimated from the initial dilution of $^{18}$O. Calculation of CO$_2$ production followed the equation of Nagy (1980), and 21.8 J/ml CO$_2$, suitable for a leaf-based diet (Kam & Degen 1997), was used to calculate energy expenditure. During measurements of FMR, body mass of the hyraxes did not differ significantly between capture and recapture (mean ± SD change: 4.26 g/day ± 4.24; N = 16; paired t test: $t_{15} = 1.004$, $P = 0.331$). Ambient temperatures during the course of the study were used to control for the effect of the environment on FMR.

Recording of Sounds and Activities

After taking the initial blood sample, we collar-fitted each male with a miniaturized digital recorder (model: Edic-mini Tiny B22; manufacturer: Telesystems Ltd, Zelenograd, Russia). Using a voice activation system, the recorder was set to start operating if the amplitude of the sound was higher than 37 dB SPL, a threshold that was found in pretrials to allow recording of sounds and activities while skipping ambient noise. When started, the recording would continue for 10 s after the last sound above this level, and the date and time of recording were saved with the file. The sampling frequency was set to 22 050 Hz, and the frequency band was 100–10 000 Hz. When the male was trapped again, we removed the recorder from his collar. Files on the recorder (range 1732–2724 files/male) were transferred to a computer for analysis. Two of us (A.I. and T.I.) then listened to all recordings and measured the length of each sound or activity. These two independent sound classifications differed by less than 1%; reclassified cases of disagreement were resolved following joint re-evaluation. Sounds were assigned to one of the following categories: sing, twitter, grunt, howl, click, bark, move (walk or run), eat, scratch and shake off (see Supplementary Material for examples). To validate our classification of sounds, we used data from visual observations of hyraxes that had been collar-fitted with miniaturized digital recorders, allowing us to link activity types and recorded sounds. We found that the recordings perfectly reflected emitted sounds, but they may have underestimated the duration of movements by failing to record quiet walking or climbing on rocks. Shaking off, scratching and barking were rare events that were not found in preliminary analysis to correlate with any other parameter, and were therefore ignored in further analyses. For each sound and activity, we calculated the average duration per day per male to compare these data among males.

We measured the amplitude of each sound using root mean square (RMS; Ritschard & Brumm 2011; Zollinger et al. 2011). The total sound energy in songs was calculated by multiplying RMS and the length of the song.

Overall, we were able to simultaneously record sounds and measure energy expenditure for 10 different males. Two males were sampled twice in consecutive years, and two others were sampled three times in three different years. Therefore, for further analysis we averaged the results of males that were sampled more than once.

Statistical Analysis

Means ± SD are presented throughout. Pearson correlations were used for all correlation tests between two parameters. A planned comparisons ANOVA was used to compare the amplitude of the different sounds. A general linear model (GLM) was used to test which parameters affected the FMR. FMR was set as the dependent variable, while the predictors were temperature (mean daily peak temperature during sampling); male age; male body mass; duration per day of the following: sing; eat; move; twitter; howl; grunt; click. Preliminary GLM analysis showed no effect of site or year. We selected among possible models using Akaike’s Information Criterion, corrected for small sample size (AICc), and Akaike weight, $w_i$ (Johnson & Omland 2004). Statistical analyses were performed using JMP 10 (SAS Institute, Cary, NC, U.S.A.) and R 2.14.2 (R Development Core Team 2011).

RESULTS

Males spent an average of 5.52 days with the attached digital recorders (range 4.1–7.9 days). Average body mass of males was 2.78 ± 0.16 kg, and mean FMR was 887.0 ± 170.3 kJ/day (N = 10). Figure S1 shows a typical activity pattern, based on the recordings from a male hyrax during the sampling period. Hyrax activities during the recorded time are summarized in Table S1. On average,
males spent 4.6 ± 1.6 min/day moving, 21.7 ± 10.4 min/day eating, 8.4 ± 5.8 min/day singing (range 1.8–21.8) and 12.4 ± 7.3 min/day producing social sounds.

Songs were significantly louder than twitters, grunts, howls and clicks (planned comparison between song and all other call types combined: F_{1,45} = 63.6, P < 0.0001; Fig. 1). Most of the variation in the sound energy was significantly explained by the mean time spent singing/day (Pearson correlation: r_8 = 0.935, P < 0.0001; Fig. 2a); therefore, we used time spent singing/day in all further analyses.

The total time per day spent moving and eating (chewing) were significantly positively correlated (r_8 = 0.700, P = 0.024), and were therefore summed in the GLM model. Grunt and click sounds were also positively correlated (r_8 = 0.785, P = 0.007) and therefore summed.

The best GLM model accounted for 84% of the variation in FMR and showed that singing time was negatively correlated with FMR. In contrast, social sounds (twitters, howls, grunts and clicks) were positively correlated with FMR (Tables 1, 2). Models in which social rank (David’s score) replaced singing duration were also supported but with a lower Akaike weight (Table 2). Models including mean daily peak temperature, hyrax body mass, hyrax age and time spent moving and eating per day were less likely to explain the observed data (Table 2).

Singing duration was not correlated with social sounds duration (Pearson correlation: r_8 = 0.045, P = 0.899), nor with any specific social sound (twitter: r_8 = 0.176, P = 0.625; howl: r_8 = 0.141, P = 0.700; click: r_8 = 0.292, P = 0.414; grunt: r_8 = 0.022, P = 0.952). In observations over 4 years (2007–2010), the number of singing events/day significantly increased with the number of aggressive encounters/day (r_{66} = 0.492, P < 0.0001).

FMR, controlled for body mass, significantly decreased with male David’s score (r_{12} = −0.557, P = 0.039; Fig. 2b; for this result we also used data from four other males for which the recorder did not work). The mean time spent singing/day significantly increased with the singer’s David’s score (r_8 = 0.699, P = 0.025; Fig. 2c). The age at death of adult males in the population significantly increased with their David’s score (r_{21} = 0.491, P = 0.024). Other activities or sounds were not correlated with David’s score (move: r_8 = 0.063, P = 0.862; eat: r_8 = 0.030, P = 0.936; grunt: r_8 = 0.017, P = 0.960; click: r_8 = 0.266, P = 0.458; howl: r_8 = 0.020, P = 0.956; twitter: r_8 = 0.245, P = 0.497).

Our study design allowed us to quantify the sounds and activities of a wild mammal in unprecedented detail. Earlier studies have relied exclusively on behavioural observations (e.g. Vehrencamp

power is well suited to be an index signal because the signal’s muscles restrict the power output (Clark 2012).

In addition, we found that factors other than singing affected FMR, providing further support for the index signal hypothesis for singing in hyraxes. Specifically, other types of sounds produced by males, namely twitter, howl, grunt and click, were positively correlated with FMR. We suggest that these latter sounds, which are not loud and are uttered a short distance from the receiver, are not costly by themselves, but rather represent social interactions with conspecifics, which involve costly behaviours (e.g. chasing, fighting) and, apparently, increase the energy expenditure (van Marken Lichtenbelt et al. 1993; Grantner & Taborsky 1998). The second best model showed that howl, a submissive sound used in social conflicts, is a good predictor of FMR (Table 1). This result suggests that weaker males may suffer higher energy costs during conflicts. Countering our prediction, we found no negative correlation between the duration of singing and the duration of social sounds. Furthermore, our observational data showed a positive correlation between the number of times males sang and the number of social conflicts. Therefore, our results do not support the hypothesis that singing reduces the need to engage in costly social interactions. Then why do some males sing less than others? The answer may lie in the fact that songs provide reliable information about the singer, in the hyrax (Koren & Geffen 2009) and in other species (e.g. koala, Phascolarctos cinereus: Charlton et al. 2011; American bison, Bison bison: Wyman et al. 2012), and thus, for weak males (e.g. small, or with low social rank), singing could be less advantageous if it advertises their weakness or elicits aggression from other males.

Our results show that energy expenditure decreased with higher male rank. Overall, field metabolic rate (total energy expenditure) comprises expenses due to intrinsic factors (basal metabolic rate plus the heat increment of feeding) and extrinsic factors (activities and behaviour). We suggest that higher-ranked males may expend less energy not due to any activity or vocalization (that altogether constitute a small proportion of the daily time budget), but rather due to lower internal metabolism. Intraspecific variation in the levels of basal metabolic rate (BMR) was found in several species (Derting & McClure 1989; Earle & Lavigne 1990; Jackson et al. 2001). Although the activities and sounds we recorded represent only the net time spent in each activity, we can state that the hyraxes in our study spent only a small portion of the time in activity, suggesting that intrinsic factors such as BMR may play a major role in their total FMR. The link between BMR and FMR is in line with the suggested relationship between personality and metabolism (Careau et al. 2008), as personality may play a role in determining social rank (Caine et al. 1983; Colléter & Brown 2011). Lower BMR in males of higher quality is also consistent with the results of McElligott et al. (2003), who found that in fallow deer, Dama dama, such males were more efficient at converting energy into reproductive success and had higher survival rates. Our results show that survival increases with social rank, supporting the link between rank and metabolism: if higher-ranked males have lower BMR, their rate of ageing is expected to be lower (Finkel & Holbrook 2000), leading to better survival. At this stage we cannot determine whether low BMR facilitates higher social rank, or whether higher social rank facilitates low BMR, possibly as a result of reduction in stress levels. Nevertheless, if higher-ranked males expend less energy due to intrinsic metabolism, then the negative correlation between singing and FMR is just a by-product of the correlation between David's score and singing duration. Although our models showed stronger statistical support for the effect of singing duration than for the effect of the David’s score on FMR, this difference may be due to the method of measurement of these two parameters. Singing duration is accurately measured from the recordings.

Table 1
The GLM results for the two best models examining effects on field metabolic rate (FMR) in rock hyrax males (see Table 2 for model selection)

<table>
<thead>
<tr>
<th>Term</th>
<th>Estimate</th>
<th>SE</th>
<th>L.R.G2</th>
<th>P</th>
<th>Net R2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Best model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Social sounds</td>
<td>0.29</td>
<td>0.05</td>
<td>14.96</td>
<td>0.0001</td>
<td>0.549</td>
</tr>
<tr>
<td>Singing</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>–0.28</td>
<td>0.06</td>
<td>11.24</td>
<td>0.0008</td>
<td>0.329</td>
<td></td>
</tr>
<tr>
<td><strong>Second-best model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Howl</td>
<td>1.39</td>
<td>0.28</td>
<td>12.55</td>
<td>0.0004</td>
<td>0.564</td>
</tr>
<tr>
<td>David’s score</td>
<td>–100.60</td>
<td>34.61</td>
<td>6.30</td>
<td>0.0122</td>
<td>0.197</td>
</tr>
</tbody>
</table>

Net R2 is the contribution to the model variance accounted for by each term after all other terms were included in the model. L-R χ² is the likelihood ratio χ².

Table 2
Model selection for the effects of activities and sounds on field metabolic rate (FMR) in rock hyrax males

<table>
<thead>
<tr>
<th>Model parameters</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sing, social sounds</td>
<td>127.67</td>
<td>0</td>
<td>0.648</td>
<td>0.0001</td>
</tr>
<tr>
<td>David’s score, howl</td>
<td>131.16</td>
<td>3.49</td>
<td>0.113</td>
<td>0.0006</td>
</tr>
<tr>
<td>Sing, howl</td>
<td>131.36</td>
<td>3.69</td>
<td>0.102</td>
<td>0.0006</td>
</tr>
<tr>
<td>David’s score, social sounds</td>
<td>132.73</td>
<td>5.06</td>
<td>0.052</td>
<td>0.0013</td>
</tr>
<tr>
<td>Sing, social sounds, temperature</td>
<td>134.25</td>
<td>6.58</td>
<td>0.024</td>
<td>0.0001</td>
</tr>
<tr>
<td>David’s score, social sounds, body mass</td>
<td>134.51</td>
<td>6.84</td>
<td>0.021</td>
<td>0.0001</td>
</tr>
<tr>
<td>Body mass, temperature</td>
<td>134.79</td>
<td>7.12</td>
<td>0.018</td>
<td>0.0035</td>
</tr>
<tr>
<td>Sing, twitter</td>
<td>135.46</td>
<td>7.79</td>
<td>0.013</td>
<td>0.0049</td>
</tr>
<tr>
<td>Sing, social sounds, move + eat</td>
<td>136.57</td>
<td>8.90</td>
<td>0.008</td>
<td>0.0003</td>
</tr>
<tr>
<td>David’s score, social sounds, age</td>
<td>141.34</td>
<td>13.67</td>
<td>0.001</td>
<td>0.0033</td>
</tr>
<tr>
<td>Twitter, howl, grunt + click, sing</td>
<td>146.57</td>
<td>18.90</td>
<td>&lt;0.001</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Social sounds include twitter, howl, grunt and click. AICc: Akaike’s Information Criterion corrected for sample size. ΔAICc: difference between each model and the best model. wi: Akaike weight (likelihood of a model relative to the others).
taken during the usage of doubly labelled water. In contrast, social rank was calculated from observations over the whole field season, and may thus reflect less accurately the social status of the male in the days when FMR was measured.

Hyrax songs tend to escalate (Kershenbaum et al. 2012), suggesting they cannot be classified as repetitive signals provided for signal validation (Mowles & Ord 2012). This leaves extrinsic cost capacity, such as predation risk, as the most reasonable cost of hyrax songs. It is still unclear as to whether there is a relationship between the type of cost (energy, risk, or time) and the type of benefit (immediate benefit versus maintenance of long-term reputation; Zuk 1991; Seary & Nowicki 2005). For example, in prey that utter an alarm call to warn group members, the cost is probably the risk of being exposed, but it is unknown whether the benefit lies in the immediate saving of kin from predation, or in creating a reputation as a valuable member of the group. In the case of rock hyrax singing, we have ruled out the energy cost. We can also preclude time as a major cost, as hyraxes in our study sang for an average of only 8.4 ± 5.8 min/day, leaving most of their time free to perform other activities. Therefore, the main cost of singing is probably that of the risk of exposure. Indeed, in many of our observations we were able to locate a male only after hearing it singing. In terms of benefit, hyraxes do not seem to gain any immediate reward after singing (Ilany et al. 2011), leaving the maintenance of reputation as the most probable benefit. Consequently, we suggest that hyrax males trade safety for reputation when singing. As our results show, this trade-off becomes worthwhile as males increase in social status.

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Supplementary Material

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