

# The Influence of Leaf Consumption on Time Allocation in Black Howler Monkeys (*Alouatta pigra*)

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## Keywords

*Alouatta* · Campeche · Foraging effort · Mexico · Reproductive state · Resting · Seasonality · Time budgets · Travelling

## Abstract

The analysis of factors that determine variation in time budgets is important to understand the interactions between environment, behaviour and fitness. We tested the hypothesis that changes in the dietary patterns of black howler monkeys (*Alouatta pigra*) caused by a decrease in the availability of preferred foods are a main determinant of variation in time budgets. We predicted that individuals would trade off travel time for resting time (i.e., minimize energy expenditure) as the diet included more leaves. We conducted our study in the Mexican state of Campeche between 2005 and 2008, where we studied the behaviour of 28 adult males and 32 adult females belonging to 14 different groups for a total of 3,747.2 focal sampling hours. Study groups lived in forest fragments with variation in habitat quality. Individuals showed different rest:travel trade-offs in response to leaf consumption according to the quality of the forest fragments they lived in. Individuals that lived in high-quality fragments increased resting time under more folivorous regimes, whereas those living in low-quality fragments increased travel time. Our results suggest that howler monkeys living in low-quality fragments spend more time foraging to compensate for the low quality of the available resources.

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## Introduction

Time allocation has a critical influence on fitness, as it influences the interaction between individuals and their environment. It has been argued that time is the most crucial constraint faced by organisms, as time allocation is a proximate mechanism

for accessing limiting resources (e.g., nutrients [Dunbar et al., 2009]). Supporting such a contention, there is evidence that geographic distribution and social organization of an animal may be predicted by time budget models [Dunbar, 1992; Lehmann et al., 2007; Korstjens et al., 2010; Bettridge et al., 2010]. Analysing which factors determine variation in time budgets is therefore important to understand the interactions between environment, behaviour and fitness.

The main components of time budget allocations are: feeding, travelling, resting and socializing [Marshall et al., 2012]. Variation in the time allocated to each of these behaviours is related to several intrinsic and extrinsic factors. Among intrinsic factors, age, sex and reproductive state have demonstrated effects on time allocation in a variety of animal species. Time spent feeding in yearling yellow baboons (*Papio cynocephalus*), for instance, varies during their 30–70 weeks of life [Altmann, 1998], and juvenile cranes (*Grus grus*) spend more time feeding than adults [Alonso and Alonso, 1993]. Concerning sex-related variation in time budgets, male Eurasian beavers (*Castor fiber*) and Przewalski horses (*Equus ferus przewalskii*) spend more time travelling than females [Boyd, 1988; Sharpe and Rosell, 2003], although age/sex differences in mountain gorillas (*Gorilla gorilla beringei*) time budgets are not notable [Watts, 1988]. Changes in female reproductive state are associated with variation in time budgets in several species. Compared to other reproductive states, feeding time decreases during lactation in black howler monkeys (*Alouatta pigra*) [Dias et al., 2011], chacma baboons (*Papio ursinus*) [Barrett et al., 2006], giraffes (*Giraffa camelopardalis*) [del Castillo et al., 2005], and siamangs (*Symphalangus syndactylus*) [Lappan, 2009] but increases in geladas (*Theropithecus gelada*) [Dunbar and Dunbar, 1988] and humans [Piperata and Dufour, 2007].

Among extrinsic factors affecting time allocation, food availability seems to be particularly important. For instance, when facing resource scarcity, animals may spend more time feeding (e.g., capuchins, *Cebus olivaceus* [Robinson, 1986]; Cat Balangurs, *Trachypithecus poliocephalus* [Hendershott et al., 2016]; chimpanzees, *Pan troglodytes verus* [Doran, 1997]; lion-tailed macaques, *Macaca silenus* [Menon and Poirier, 1996]; tarsiers, *Tarsius spectrum* [Gursky, 2000]; Western lowland gorillas, *Gorilla gorilla gorilla* [Masi et al., 2009]), or more time resting (e.g., moose, *Alces alces* [Sæther and Andersen, 1990]).

However, as time is inelastic, changes in one time budget component imply trade-offs with other behaviours. Time budget trade-offs caused by food scarcity are usually associated with 1 of 2 possible energetic strategies: a high-investment/high-return strategy, whereby individuals devote more time to search for preferred foods; low-investment/low-return strategy, in which individuals switch their diet towards food items that are more abundant, although of lower quality (i.e., fallback foods [Marshall et al., 2009]). Both strategies should in principle involve a trade-off between resting and travelling time: when using the high-investment/high-return strategy individuals prioritize travelling because the higher energetic expenditure of travelling is offset by higher energy intake; when using the low-investment/low-return strategy individuals prioritize resting because the lower energy intake limits energy expenditure.

Changes in time budgets in response to food scarcity entail costs (e.g., increasing travel time to find food increases predation risk [Bettridge et al., 2010]), but because food shortages are usually short-term and predictable, these costs are acceptable and time budget changes are adaptive. However, under extreme food shortages, behav-

joural changes may be insufficient to ensure individual reproduction and survival. Such is the case, for example, of individuals facing prolonged droughts, hurricanes, and forest fires [Decker, 1994; Pierson et al., 1996; O'Brien et al., 2003]. Halfway between these scenarios (i.e., short-term, predictable food scarcity and extreme scarcity) are human-induced food shortages. Anthropogenic disturbance changes habitat patterns and, with it, induces variation in food availability [Tylianakis et al., 2008]. Adjustments in time budgets in response to anthropogenic disturbance have been documented in several taxa and may involve either of the two energetic strategies described above (e.g., black bears, *Ursus americanus* [Beckmann and Berger, 2003]; chimpanzees, *Pan troglodytes* [Bryson-Morrison et al., 2017]; mantled howler monkeys, *Alouatta palliata* [Asensio et al., 2007]; Florida scrub-jays, *Aphelocoma coerulescens* [Fleischer et al., 2003]; spider monkeys, *Ateles geoffroyi* [Ordóñez-Gómez et al., 2016]; Sulawesi Tonkean macaques, *Macaca tonkeana* [Riley, 2007; but see Bishop et al., 2015]). It is less clear, however, which are the specific factors determining such adjustments.

In the present study, we tested the hypothesis that changes in dietary patterns of black howler monkeys (*A. pigra*) caused by a decrease in the availability of preferred foods (fruits [Dias and Rangel-Negrin, 2015a]) are a main determinant of variation in time budgets. We have previously demonstrated that food availability for black howler monkeys decreases as forest fragments become smaller, due to a reduction in the size and diversity of food sources [Dias et al., 2014]. Under these circumstances, individuals increase leaf consumption. Infant mortality and physiological stress increase as fragments become smaller, and population growth decreases [Rangel-Negrin et al., 2014; Dias et al., 2015a]. Howler monkeys prefer consuming fruits whenever these are available [Silver et al., 1998; Stevenson et al., 2000; Palma et al., 2011], and there is evidence that physical condition is poorer in individuals that consume more leaves [Espinosa-Gómez et al., 2013; Dias et al., 2017]. Therefore, it is possible that the documented relationship between anthropogenic disturbance and both physiological stress and population parameters is mediated by the effect of leaf consumption on time budgets (i.e., individuals not meeting their energetic requirements under a strictly folivorous diet). Accordingly, because leaves provide less energy than fruits [Righini et al., 2017], we predicted that as diet becomes more folivorous individuals should trade off travel time for resting time (i.e., show a low-investment/low-return time budget strategy).

## Methods

### *Ethics Statement*

We conducted this study in accordance with protocols approved by Universidad Veracruzana, and adhered to the legal requirements of the Estados Unidos Mexicanos (SEMARNAT SGPA/DGVS/01273/06 and 04949/07).

### *Study Sites and Subjects*

We studied black howler monkeys in the state of Campeche (Yucatán Peninsula, Mexico) from April 2005 to November 2008. In Campeche, the climate is hot and humid [Vidal-Zepeda, 2005], and the mean annual rainfall is 1,300 mm, with a dry season from November to May ( $43.7 \pm 25.8$  mm), and a rainy season between June and October ( $218.9 \pm 14.1$  mm). The mean annual temperature is  $26^\circ\text{C}$ .

**Table 1.** Attributes of the forest fragments and of the black howler monkey groups studied in Campeche (Mexico) from April 2005 to November 2008

Group	Fragment size, ha	Distance to nearest fragment, m	Sum of basal areas of trees <sup>a</sup> , cm	Plant species richness <sup>a</sup>	Percent plant species typical of mature forests <sup>a</sup>	Group size <sup>b</sup>
<b>Low-quality habitats</b>						
AA Álamo	35.3	2.6	1,334.8	17	31.5	4 (2/2)
Atascadero	1.2	101.1	962.4	15	36.4	4 (2/1)
Chicbul	5.0	6.2	1,436.2	16	37.5	5 (1/2)
Chilar	2.1	25.2	1,200.1	4	14.2	8 (2/3)
Manantiales	50.0	94	1,626.1	22	15.9	3 (1/1)
Oxcabal	7.0	339.1	1,436.2	5	50.9	6 (3/2)
R Álamo	96.0	50.7	1,656.2	25	52.5	8 (1/4)
Subestación	6.0	203.7	1,343.1	13	25.0	5 (2/2)
Mean ± SE	25.3±11.9	102.8±41	1,374.4±79.4	14.6±2.6	33.0±5.1	5.4±0.7 (1.8±0.3/2.1±0.4)
<b>High-quality habitats</b>						
Calakmul S	140,000	30	3,353.7	33	71.6	5 (1/2)
K9 Calakmul	51,503	30	3,003.9	22	76.0	5 (2/2)
Calaxchil	3,000	4.3	2,577.9	24	51.2	6 (1/2)
T61 Calax	300	164.6	2,237.9	25	55.4	9 (2/3)
Tormento N	600	38.8	1,920.8	26	67.6	10 (3/4)
Tormento S	800	38.8	2,650.4	29	62.9	6 (2/2)
Mean ± SE	32,700.5± 22,983.1	51.1±23.3	2,624.1±210.0	26.5±1.6	64.1±3.9	6.8±0.9 (1.8±0.3/2.5±0.3)

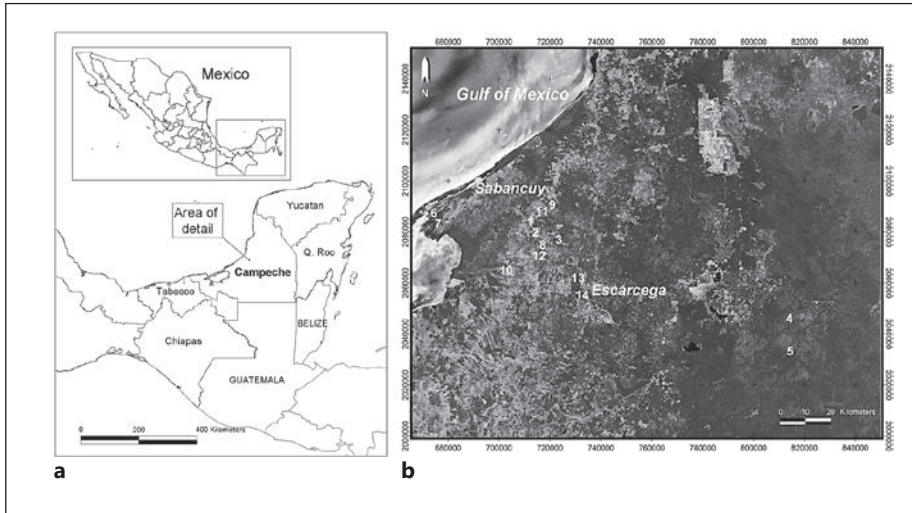
Figures in parentheses represent the number of adult males and females per group (i.e., males/females). <sup>a</sup> Determined through ten 50 × 2 m linear transects inside each group's home range [Dias et al., 2014, 2018]. <sup>b</sup> Calculated through direct counts of individuals [Dias et al., 2015a, b].

We studied 14 groups of black howler monkeys that lived in different locations in Campeche [described in Dias et al., 2014, 2015a, 2016, 2018] (Table 1; Fig. 1). We have previously demonstrated that size is a good predictor of the quality of forest fragments for black howler monkeys, as attested by lower infant mortality, lower extinction probabilities and higher population growth in bigger fragments [Dias et al., 2014, 2016, 2018]. In fragments larger than 100 ha, tree basal area, plant species richness, and the proportion of plant species typical of mature forests increase [Dias et al., 2014, 2018], suggesting that in these fragments food availability is higher. Therefore, in the present study we classified each fragment as high ( $n = 6$ ) or low ( $n = 8$ ) quality according to its size (Table 1).

We studied the behaviour of 25 adult males and 32 adult females (Table 1). We individually recognized all subjects on the basis of their natural anatomical and physiognomic characteristics, such as body size and proportions, scars, broken fingers and genital morphology and pigmentation. We classified females according to their reproductive state as cycling (females not gestating or lactating), gestating (females in the period encompassing the day before parturition to 184 days back from that date, which corresponds to the mean duration of pregnancy in this species [Van Belle et al., 2009]), or lactating (females with a <14-month-old associated infant).

#### *Behavioural Sampling*

We collected 1-h focal-animal continuous recordings [Altmann, 1974] of the behaviour of adult individuals. During focal sampling, we recorded the time dedicated to rest (sleep or static without social interaction), travel (movement to a different area or tree), feed (inspection of food,



**Fig. 1.** Map of Mexico (**inset**) showing the Yucatán Peninsula. We worked in Campeche (**a**) where we studied 14 groups of black howler monkeys living in 14 forest fragments. **b** The approximate location of each group is depicted as a number.

bringing food to mouth, chewing and swallowing, moving while feeding within a food patch), and socialize (affiliative and agonistic social interactions as defined in Dias and Rangel-Negrín [2015b]). During feeding, we recorded the food item consumed (fruit, leaf, flower, and other). Observations were performed during complete days (i.e., 6:00–17:00 or 7:00–18:00, depending on daylight during the year). Within each group, we selected focal animals on a pseudorandom basis, such that we did not sample an individual twice until all were sampled once, and focal samples of each animal were evenly distributed throughout the day. We collected a total of 3,747.2 focal hours, with a mean ( $\pm$ SD) observation time of  $62.5 \pm 19.8$  h per individual and  $267.7 \pm 39.71$  h per group. We sampled each group for approximately 1 month in each season (i.e., dry and rainy seasons).

#### *Data Organization and Analysis*

We multiplied time spent eating each food item by intake rates (g/min) previously calculated for this species [Amato and Garber, 2014] to obtain an estimation of the amount of ingested food (in grams) per plant part. From these data, we calculated the percentage of ingested leaf weight per individual per season. We calculated the trade-off between rest and travel as the ratio of time each individual spent resting to time spent travelling per season (rest:travel trade-off hereafter).

We used a linear mixed model [West et al., 2014] to explore the effect of leaf consumption, the interaction between leaf consumption and fragment quality, and the interaction between leaf consumption and season (i.e., fixed factors) on rest:travel trade-off. As there is evidence that the time budgets of howler monkeys vary among female reproductive states [Dias et al., 2011; Cano-Huertes et al., 2017], we also included in the model the interaction between leaf consumption and sex/reproductive state (i.e., male, cycling female, gestating female, lactating female). In this model, we included subject identity as a random factor to account for the values of the same individuals in the 2 seasons and entered observation time per individual per season as an offset variable. We verified the underlying assumptions of the model visually with Q-Q plots of residuals fitted against predicted values. Rest:travel trade-off and leaf consumption had normal distributions after logarithmic and arcsine-square-root transformations, respectively (assessed with Shapiro-

**Table 2.** Linear mixed model explaining variation in the trade-off between resting and travelling time in 14 groups of black howler monkeys studied in Campeche (Mexico) from April 2005 to November 2008

Factor	B	SE	df	$\chi^2$	<i>p</i>	95% CI	
						lower	upper
Leaf consumption	0.45	0.22	1, 108.7	1.9	0.169	0.01	0.89
Leaf consumption × fragment quality	-0.38	0.09	1, 73.6	18.9	<0.001	-0.56	-0.21
Leaf consumption × season	-0.11	0.09	1, 69.2	1.6	0.210	-0.29	0.06
Leaf consumption × sex reproductive state	-0.03	0.21	3, 90.5	0.8	0.860	-0.44	0.38

Wilk tests). We used R package “lme4” [Bates et al., 2017] with function “lmer” to obtain model parameters, and with function “confint” to obtain confidence intervals for the estimates of fixed factors. For significance testing, we first used a likelihood ratio test to compare a null model including only the random factor with a full model including all fixed factors mentioned above (R package “stats” [R Core Team, 2017]). We then used function “anova” from package “car” [R Core Team, 2017] to calculate *p* values for each fixed factor. We calculated pseudo-R-squared to assess effect size (R package “sjstats” [Lüdtcke, 2017]). When interaction effects were significant, we ran an independent mixed model for each interaction term using subject identity as a random factor.

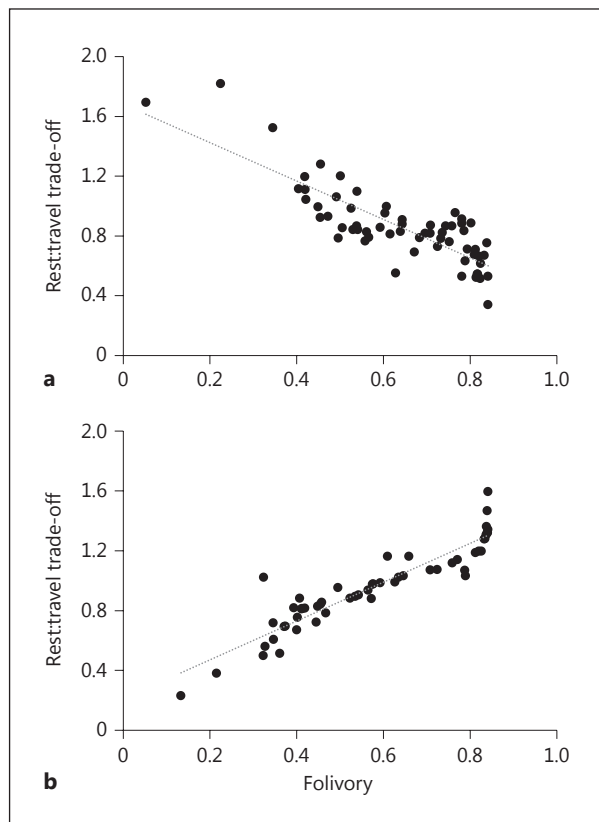
## Results

Rest:travel trade-off varied between 1.7 and 78.4 (mean ± SD = 11.1 ± 12.9), and was lower (i.e., more time travelling) in the dry (8.9 ± 10.3, range = 1.7–68.5) than in the rainy season (13.3 ± 14.9, range = 3.2–78.4), and in low-quality (9.3 ± 10.1, range = 2.2–65.7) than in high-quality fragments (13.2 ± 15.4, range = 1.7–78.4). Rest:travel trade-off was higher in males (11.8 ± 14.6, range = 3.1–68.5), followed by lactating (10.9 ± 13.7, range = 1.7–78.4) and cycling females (10.3 ± 3.9, range = 6.5–20.2), and, finally, by gestating females (8.8 ± 4.6, range = 2.2–15.6).

The model including all predictors (i.e., leaf consumption, interaction between leaf consumption and fragment quality, interaction between leaf consumption and season, and interaction between leaf consumption and sex/reproductive state) was significantly different from the null model including only subject identity as a random factor ( $\chi^2_6 = 29.9$ ,  $p < 0.001$ ) and explained 25% of the variation in rest:travel trade-off ( $R^2 = 0.25$ ). The interaction between leaf consumption and fragment quality had a significant effect on rest:travel trade-off ( $F_{1, 73.6} = 18.7$ ,  $p < 0.001$ ; Table 2). Specifically, rest:travel trade-off was negatively related with leaf consumption in low-quality fragments ( $F_{1, 56.6} = 25.28$ ,  $p < 0.001$ ; Fig. 2a). In contrast, rest:travel trade-off increased with increased leaf consumption in high-quality fragments, indicating that individuals spent more time resting ( $F_{1, 48.4} = 55.1$ ,  $p < 0.001$ ; Fig. 2b). Rest:travel trade-off was not affected by leaf consumption per se, season, and by subject sex/reproductive state.



**Fig. 2.** The relationship (linear mixed model) between leaf consumption and the trade-off between resting and travelling time in 14 groups of black howler monkeys studied in Campeche (Mexico) from April 2005 to November 2008: individuals living in low-quality forest fragments (**a**); individuals in high-quality fragments (**b**). Trend lines are shown only for visualization purpose.



## Discussion

Our results suggest that the trade-off between resting and travelling time is not generally affected by leaf consumption per se in black howler monkeys. However, in high-quality fragments individuals traded off travelling for resting time under a more folivorous diet, whereas higher leaf consumption resulted in less time resting in low-quality fragments. Time allocation was unaffected by the interaction between leaf consumption and either climatic seasonality or sex/reproductive state of individuals. Our results provide evidence that time budget trade-offs in this species are linked to a combination of diet and habitat features.

Leaf consumption per se had a non-significant effect on the rest:travel trade-off of black howler monkeys in our study. Instead the effect of leaf consumption on time budget trade-off was modulated by fragment quality. Previous research has indicated that anthropogenic habitat disturbance could impact primate time budgets in a variety of ways [Palma et al., 2011; Ordóñez-Gómez et al., 2016; Mekonnen et al., 2017], but our study is possibly the first to provide evidence of a link between leaf consumption and variation in energy budget strategies depending on habitat quality: from a low-investment/low-return strategy in high-quality fragments to a high-investment/low-

return budget in low-quality fragments. Such variation could imply less net energy available under a more folivorous diet, as leaves, although rich in proteins and minerals [Ganzhorn et al., 2017], tend to have lower energy content than fruits, and howler monkeys would obtain less energy [Silver et al., 2000]. This, coupled with increased travelling time, implies higher energy expenditure [Dunn et al., 2013; Dias et al., 2017].

Previous studies of black howler monkeys in Campeche have found evidence that, similarly to what has been reported in other primates [Mbona et al., 2009; Puig-Lagunes et al., 2016; but see Umaphathy et al., 2011], several population parameters (e.g., group size, population growth, infant survival) are negatively affected by a decrease in fragment size and an increase in habitat disturbance [Dias et al., 2015a], and subpopulations are predicted to be unviable (i.e., are losing individuals and will probably become extinct in the short term [Dias et al., 2015b]). These negative effects might be a direct consequence of individuals not meeting their nutritional requirements due to a decrease in food availability [Dias et al., 2015a, b] and higher leaf consumption in smaller fragments [Dias et al., 2014]. Our results suggest that the availability of less net energy associated with a high-investment/low-return energy budget could be linked to the reported negative population parameters in small, disturbed forest fragments. Because howler monkeys have a limited ability to maintain a predominantly folivorous diet [Milton, 1998], it is possible that an increase in leaf consumption enforces resting time (in this case, resting time required for digestion [Dunbar and Sharman, 1984]), limiting the time budget of individuals in all sex/reproductive state classes. This could explain why the interaction between sex/reproductive state and leaf consumption was not a significant predictor of rest:travel trade-off. As lactating females face particularly high energetic demands [Dias et al., 2011], inability to adjust time budgets, and consequent less net energy available, could lead to the observed lower fecundity in smaller forest fragments [Dias et al., 2015a]. Therefore, in addition to converging with previous evidence of variation in time budgets in relation to habitat disturbance in howler monkeys [Clarke et al., 2002; Asensio et al., 2007; but see Cristóbal-Azkarate and Arroyo-Rodríguez, 2007], our results suggest that the study of time budgets may be informative of the responses of individuals to anthropogenic disturbance and, thus, could help in assessing its consequences on energy allocation.

It has recently been documented that energy production by gut microbiota may compensate for reduced energy intake in black howler monkeys during lean periods [Amato et al., 2015], and that microbiota diversity varies between primary and secondary forests [Amato et al., 2016]. Future research should determine whether this microbiota variation could buffer the costs of the high-investment/low-return energy budget of black howler monkeys living in low-quality fragments. However, as survival and reproduction decrease in low-quality fragments [Dias et al., 2015a, 2016] microbiota buffering may be insufficient to promote a positive energy balance, at least in small forest fragments.

In summary, black howler monkeys showed different rest:travel trade-offs in response to leaf consumption and habitat quality. Individuals that lived in high-quality fragments increased resting time under a more folivorous diet (i.e., had an energy-minimizing strategy), whereas individuals living in low-quality fragments increased travel time. Therefore, individuals living in low-quality fragments may have less net energy available. This could explain why in small forest fragments lower population growth, lower fecundity, higher physiological stress levels and lower viability have been reported.



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## Disclosure Statement

The authors declare that they have no conflict of interest.

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