

Differential Parasitism Between Two Suitable Cowbird Hosts

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Abstract: Host choice by the brood parasitic Brown-headed Cowbird (*Molothrus ater*) is an evolved response to host suitability, resulting in patterns of differential parasitism rates among species within a community. In the ponderosa pine (*Pinus ponderosa*) forests of the Colorado Front Range, we recorded that Western Wood-pewee (*Contopus sordidulus*) is infrequently parasitized (1%, n = 259 nests) by the Brown-headed Cowbird, whereas the Plumbeous Vireo (*Vireo plumbeus*) is heavily parasitized (51%, n = 292). To account for differences in parasitism rates on these species we experimentally parasitized pewee nests with cowbird eggs, and we compared host aggression towards cowbird models, host nest attentiveness, nest placement, and egg-laying dates in these species. Pewees accepted cowbirds eggs and reacted more aggressively towards the cowbird model than the control model, were more attentive at their nest sites than vireos, and placed their nests higher and closer to the trunk than vireos. Egg-laying dates for vireos and cowbirds overlapped more than the egg-laying dates for pewees and cowbirds. We suggest that temporal asynchrony in host availability, coupled with differences in nest placement and behavior at the nest, help to account for the observed differences in parasitism rates between these two species.

Keywords: Brood parasitism, brown-headed cowbird, *Contopus sordidulus*, *Molothrus ater*, plumbeous vireo, *Vireo plumbeus*, western wood-pewee.

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*, hereafter “cowbird”) is an obligate, generalist brood parasite that generally reduces the reproductive success of its hosts [1-4]. However, for an avian community made up of several suitable host species (i.e., able to fledge cowbird young) parasitism rates among these species can be quite variable. Several factors that may explain these differences in parasitism rates include nest placement and nest concealment [5, 6], nest defense [7, 8], nest attentiveness [9], ejection of foreign eggs from the host nest [10, 11], nest abandonment [12-14], spatial nesting pattern such as colonial nesting [15, 16], host activity during nest building [17], overlap of the nesting cycles of cowbird and host [18], and host quality [19].

As part of a long-term avian monitoring program in the ponderosa pine (*Pinus ponderosa*) forests of Boulder County, Colorado, we observed two common species with quite different rates of parasitism. The Western Wood-pewee (*Contopus sordidulus*; hereafter, “pewee”) is not heavily parasitized by cowbirds although there is local variation across their range [20, 21]. In Boulder County we have found only three parasitized pewee nests over 22 years of monitoring and none of those individuals have successfully fledged. By contrast, the Plumbeous Vireo (*Vireo plumbeus*; hereafter, “vireo”) was parasitized at a 51% frequency (n = 292) [this study; 19, 22], which is more typical of published parasitism rates throughout the vireo’s range varying from

32.3% to 87% depending on habitat [23-25]. In our study area, habitat cannot account for this difference in parasitism because both species live in close proximity to each other, within the same habitat and often occupying overlapping territories. We examine here whether differences in cowbird egg ejection, host aggression towards nest intruders, host nest attentiveness, nest placement, and breeding season asynchrony between cowbird and host may account for the observed pattern of differential parasitism rates.

Ejection of cowbird eggs is a relatively uncommon yet effective parasite defense [9, 26, 27], whereby the host removes the cowbird egg from the nest by grasp-, or puncture-ejecting [1, 27]. In New Mexico, Curson *et al.* [28] demonstrated experimentally an 80% cowbird egg acceptance rate by pewees in a habitat where pewees naturally sustain a 16% parasitism rate. We tested responses of pewees to the addition of cowbird eggs to their nests. If pewees accept most cowbird eggs placed in their nests we would conclude that the species is an acceptor. However, if a significant level of rejection is demonstrated it would suggest that cowbird eggs are frequently ejected before researchers next inspect nests [c.f., 29] and indicate rejection as a factor contributing to the lack of parasitism we observed for this species.

Aggressiveness towards nest intruders is a ubiquitous nest defense behavior. However, evidence for the effectiveness of aggression in deterring cowbirds and preventing parasitism is equivocal, and some species are heavily parasitized despite their aggression [1, 8, 30, 31]. In order for aggression to be effective in preventing parasitism, the host must be in a location that facilitates interception of an intruding cowbird before it can parasitize. If a host is absent when a cowbird approaches the nest, the cowbird effectively by-

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passes any potential aggressiveness. We examine aggression at the nest as well as nest attentiveness. Hosts that leave nests absent for extended periods are susceptible to cowbirds “freely” parasitizing their nests in the absence of any host response [32, 33]. If hosts are attentive to the nest without outwardly revealing the nest, they may have an advantage over other hosts at deterring parasitism. We hypothesized that higher levels of nest attentiveness and higher levels of discriminate aggression towards cowbirds would correlate with lower parasitism rates.

If cowbirds use perches to search for nests, then particular nest heights render some nests more susceptible to parasitism than others [18, 34]. We measured nest heights and location to determine if this is a factor in the difference in parasitism frequency between pewees and vireos. In our area, the predominantly observed nest searching method by cowbirds involved females, often accompanied by males, flying among the tops of ponderosa pine trees and looking down among the trees in attempt, it appears, to locate nests or flush birds [1, 35, pers. obs]. From this high vantage point, we predicted that it would likely be easier for a cowbird to see nests on the periphery of the tree rather than on proximal branches, making the latter nests more susceptible to parasitism.

Dufty and Wingfield [36] showed that cowbird egg-laying is synchronized with primary hosts, and lower parasitism rates occur among asynchronous breeders. Breeding synchrony has been used to explain differential host use by sympatric cowbirds [25]. We examined asynchrony in the breeding season and predicted that differences in parasitism rates observed between these two species are influenced by a temporal disparity between clutch initiation dates.

MATERIALS AND METHODOLOGY

Study Area

We conducted this study during the 1984-1986, 1997-2000, 2006, and 2009 breeding seasons (May-August) in approximately 5 km² of ponderosa pine habitat within the foothills of Boulder County, Colorado (39° 57' N, 105° 17' W). The dominant vegetation was ponderosa pine with scattered Douglas fir, *Psuedotsuga menziesii*, and an open understory of shrubs including bearberry, *Arctostaphylos uva-ursi* and wax currant, *Ribes cereum*, cactus, *Opuntia compressa* and grasses, *Poa spp.* Pewee and vireo nests were found in all stages of the nesting cycle, and inspected at least once every three days. Care was taken to minimize disturbance and not to attract cowbirds and nest predators to the nest site. All nests were inspected until cowbird or “host” young fledge, were preyed upon or became otherwise inactive.

Egg Ejection

We conducted egg ejection experiments in 1997 and 1998 to determine the response of pewees to a cowbird egg placed in the nest. We did not conduct egg ejection experiments on vireos as the species is heavily parasitized in our study area and it is thus an acceptor species [22]. A single, fresh cowbird egg collected from a nearby vireo nest was placed into each of 12 pewee nests [as per 33-37]. We ob-

served nests continuously for one hour after the “parasitism”, checked nests the following day and then every other day for five days; if the cowbird egg was still present, we removed it on the sixth day. Each egg was carefully inspected for cracks, flecks, scratches or any other marks that could have been associated with an attempted grasp- or puncture-ejection [27, 38]. Individuals that accept parasitic eggs in their nests for five days were considered to be acceptors [1, 39]. Each pewee nest was in the egg-laying or early incubation stage, and eggs were placed in nests before noon because cowbirds typically parasitize nests in the morning [9, 39, 40]. One cowbird egg was left in a nest to determine whether pewees could hatch a cowbird egg. This nest was monitored until the fate of the egg and nest were determined.

Aggression

In 1997-1999 we compared pewee and vireo reactions towards cowbirds by use of female cowbird models and female house sparrow, *Passer domesticus*, taxidermic mounts, the latter as a non-threatening control of similar size to female cowbirds (*M. a. artemisiae*) in our region. We presented the models to six pewee and six vireo nests following protocols of Smith *et al.* [41] and Ortega and Cruz [33]. Nests tested with models used were not used in egg ejection experiments and nest attentiveness observations.

We placed models within one meter, at the same height, and facing each nest. Nests were in clutch initiation or early incubation, and all experiments were conducted before noon. The order of model presentation was randomized to avoid biased responses associated with presentation order. A minimum of one hour and a maximum of 24 hours separated model presentations at the same nest. We observed models while concealed behind vegetation locations more than 10 m from each nest. Experiments ran for four minutes but were terminated if models were being damaged by attacks.

When both individuals of a nesting pair engaged in observable behavior, only the behavior of the more aggressive individual was recorded because it was impossible for a single observer to document behaviors of two birds simultaneously. Behaviors were grouped into four categories that represented interpreted levels of aggression. The lowest level of aggression [1] “out of sight” - indicates a bird was hidden from the observer, unobservable, and may have been far from the nest. The highest level of aggression [4] includes behaviors involving physical contact with the model: ‘hover and bill snap’, ‘swoop and contact’, and ‘perch and peck’. Intermediate categories consist of behaviors that are mixtures of aggressiveness and nest proximity. We analyzed behaviors within and among species by the use of Wilcoxon Signed Rank Test [42] as the data were not normally distributed. Because pewee and vireo behavior are not identical (for example, pewees hovered and snapped their bill just above the models but vireos never exhibited this behavior), we assigned the highest level of aggression for the pewee: ‘swoop and contact’, ‘hover and bill snap’, and ‘perch and peck’, and for the vireo ‘swoop and contact’ and ‘perch and peck’.

Nest Attentiveness

We compared distance to nest for nine pewee and nine vireo pairs in 1998-1999, and 2009 by documenting the dis-

crete distance pairs were observed from their nests during 30-minute observations. We estimated distance by locating the bird visually and comparing these locations with pre-measured distances, placing the nearest individual as “close” (0-20 m) or “far” (> 20 m) from the nest. The park-like open-canopy forest structure facilitated these measurements and facilitated detection and following of non-vocalizing birds possible. 20 m was chosen as the distance from which all sampled vireo and pewee nests could be seen in the ponderosa pine forest, making the approach by a predator or parasite visually detectable by one member of the nesting pair. Beyond 20 m nests became increasingly more difficult to observe. When one of the pair was incubating we noted it and used the measure of distance on the other member of the pair; when the nest was not incubated we measured the distance of the individual closer to the nest. We observed from a stationary, concealed location approximately 10 m from nests. Thirty-minute observations took place between 30 min prior to dawn to 1100 MST. Nests used were unique to those used for egg ejection and nest aggression experiments. Data from the nine pewee and nine vireo nests were pooled across years and time spent within and beyond 20 m from the nest was compared with goodness of fit G-test adjusted with a Williams correction.

Nest Placement

We measured nest height of all nests in all years of study using either a clinometer or measuring tape (depending on height) and reported as mean \pm SE. Differences in nest height are reported as a percentage of total tree height, and the distance of each nest from the trunk as a percentage of branch length [43].

Breeding Asynchrony

We examined breeding asynchrony based on the date of the first observed egg as a measure of clutch initiation for field data from 1984-2006. We counted an egg as first laid only if we located a nest with no eggs and then observed the first egg on a subsequent visit, back-dating when necessary. We summed egg totals of each date into a cumulative total, and ran a Pearson correlation coefficient test between vireos and cowbirds, pewees and cowbirds, and vireos and pewees, and a Fisher z transform to compare the correlation coefficients to each other.

RESULTS

Egg Ejection

All 12 eggs placed into pewee nests were accepted. We found no signs of rejection or attempted rejection. The cowbird egg that remained in the nest hatched, but the nest was depredated shortly afterwards.

Aggression

Pewees exhibited significantly more behaviors categorized at the highest aggression level (perch and peck) towards the cowbird than towards the control model ($Z = -2.37$, $P = 0.02$). Vireos tended to respond more aggressively towards the cowbird than the control ($Z = -1.83$, $P = 0.07$). No other comparison of level of aggression elicited from models yielded statistically significant results.

Nest Attentiveness

Pewees spent more time within 20 m of the nest than vireos ($G_{ADJ} = 4.4649$, $df = 1$, $P < 0.05$; Fig. 1). For all pre-dawn observations, female pewees were incubating, thus distances to nest reflect the location of the foraging male. Male and female vireos incubate, thus the distance from the nest reflects the distance of the non-incubating individual.

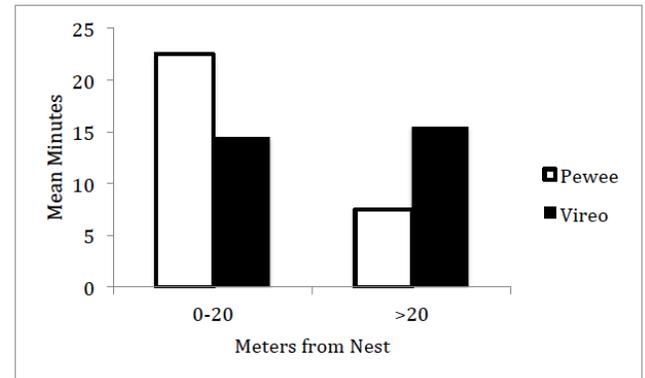


Fig. (1). Average time (min) that pewee ($n = 9$) and vireo ($n = 9$) pairs were observed at discrete distances (m) from the nest during thirty-minute observations.

Nest Placement

Pewee nests were located in larger trees (mean dbh = $44.1 \text{ cm} \pm 0.98 \text{ se}$, $n = 103$) than vireo nests ($27.9 \pm 2.47 \text{ cm}$, $n = 43$; Wilcoxon $z = 5.5924$, $P < 0.001$), in taller trees ($14.17 \pm 0.34 \text{ m}$, $n = 98$) than vireos ($9.00 \pm 0.70 \text{ m}$, $n = 40$; $z = 5.8812$, $P < 0.001$), and in trees that were generally taller than the average canopy ($109.0 \pm 2.22 \%$ of average canopy height, $n = 89$) than vireo nests ($85.0 \pm 9.93 \%$, $n = 38$; $z = 4.2181$, $P < 0.001$). Pewee nests were found higher ($4.83 \pm 0.24 \text{ m}$, $n = 101$) than vireo nests ($2.67 \pm 0.19 \text{ m}$, $n = 43$; $z = 5.3027$, $P < 0.001$) and closer to the trunk ($56.1 \pm 1.59 \%$ of total distance trunk to tip, $n = 106$) than vireo nests ($75.3 \pm 3.31\%$, $n = 43$; $z = 6.3411$, $P < 0.001$).

Breeding Asynchrony

Vireo and cowbird egg laying dates show a greater correlation ($r = 0.99648$, $P < 0.0001$), than pewee and cowbird ($r = 0.92543$, $P < 0.001$) or the pewee and vireo ($r = 0.90576$, $P < 0.001$; Fig. 2). The correlation coefficient between the egg laying date of vireos and cowbirds was significantly different than that for pewees (vireo and cowbird vs. pewee and cowbird, $z = 8.15$, $P < 0.001$; vireo and cowbird vs. vireo and pewee, $z = 8.84$, $P < 0.001$; pewee and cowbird vs. vireo and pewee $z = 0.69$, $P = 0.25$), showing that these two species (cowbird and vireo) strongly overlap. A 13-day lag exists between the first egg laid by a vireo and pewee.

DISCUSSION

Egg Ejection

Species that eject cowbird eggs tend to have parasitism rates lower than 10% [44]. Observers might miss parasitic events because cowbirds eggs have been removed from the nest by the hosts, a behavior known as cowbird egg ejection

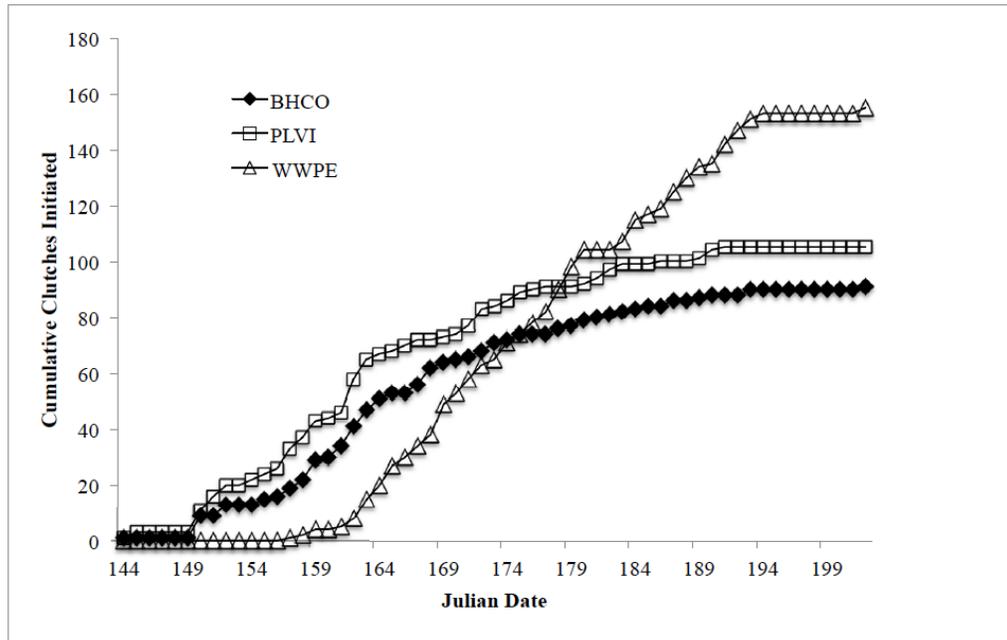


Fig. (2). The number of cumulative clutches laid by brown-headed cowbirds (BHCO), plumbeous vireos (PLVI), and western wood-pewees (WWPE) throughout the breeding season in the ponderosa pine (*Pinus ponderosa*) foothills west of Boulder, Colorado (1984-2006).

[10, 29, 39, 45]. Therefore the hypothesis that a potential host species recognizes and rejects cowbird eggs must first be tested before alternative hypotheses can be explored. In Boulder, Colorado, pewees are rarely parasitized by cowbirds [19, this study]. We found pewees accepted all experimental cowbird eggs placed into their nests, and thus egg ejection is ruled out as a contributing factor for the low levels of parasitism observed in the pewee. These results in conjunction with the experimental parasitism work in New Mexico [28] confirm that the Western Wood-pewee is a cowbird egg acceptor and are similar to cowbird egg acceptance recorded for the Eastern Wood-pewee (*C. virens*) [18].

Aggression

Both pewee and vireo responded aggressively towards cowbird and House Sparrow models at the nest. Pewees exhibited significantly more aggression towards the cowbird model than towards the House Sparrow, indicating that pewees recognize the cowbird as a specific threat [46]. While the effectiveness of such behavior is unclear [8], there are instances where midwestern Bell's Vireos (*Vireo bellii*) have been known to deter parasitism through aggressive encounters with cowbirds [47]; although Sharp and Kus [48] provide evidence to the contrary where such responses fail to deter cowbirds from parasitizing Bell's Vireo nests in California. In Colorado, both pewee and vireos are aggressive towards cowbirds, and yet only the vireos are parasitized. Perhaps pewees, which tend to spend more time near the nest, recognize nest-searching cowbirds and drive females away before they can find or inspect nest contents.

Nest Attentiveness

Pewees were more attentive at the nest than vireos. Being on the nest at dawn might be one defense against parasitism [9]; however, these authors [9] found no correlation between

sunrise nest attentiveness and frequency of parasitism in a community of ten potential cowbird hosts in Manitoba, including the cowbird-accepting Least Flycatcher (*Empidonax minimus*). Despite being off the nest during the critical period of clutch initiation, parasitism of the Least Flycatcher was very low [9]. Sealy *et al.* [49] found that sunrise nest attentiveness may be a function of incubation rather than a specific response to parasitism in the Yellow Warbler (*Setophaga petechia*). However, other hosts, such as the Yellow Warbler, may recognize the cowbird threat and sit on the nest when cowbirds approach [46, 50]. For hosts smaller than the cowbird, such as the Least Bell's Vireo (*Vireo bellii pusillus*) defense of the nest may still result in parasitism by the larger cowbird [48].

Perhaps the key element for deterring cowbird parasitism is host vigilance around the nest during dawn cowbird egg-laying, and throughout the day, when female cowbirds are searching for nests to parasitize by inspecting their contents, parasitizing them at dawn on a subsequent morning [51]. Cowbirds fly directly to host nests at sunrise to lay eggs [9, 52], indicating that females have identified potential nests in the critical stage of clutch initiation at least the day prior to laying. Nest-searching female cowbirds may be distracted or chased from nest sites by vigilant potential hosts. In the case of pewees and vireos studied here, the distance from the nest by pewees was closer than among vireos (Fig. 1), which perhaps allowed them to detect and deter female cowbirds from approaching nests. Focal individuals during this part of our study were probably males, where females were most likely incubating eggs. While we did not quantify the male's behavior, they were often singing and foraging. The difference in their insectivorous foraging behavior, vireos typically leaf glean, whereas pewees sally-hover flying insects, may explain both their time spent near the nest and their vigilance towards potential intruders in the territory. Nest-site vigilance coupled with highly aggressive responses towards

cowbird models may be enough for pewees to escape or minimize parasitism.

Nest Placement

Vireo and pewee nests are generally unconcealed in the semi-open ponderosa pine savanna habitat of Boulder, Colorado. Pewee nests tend to be located higher in larger trees and placed on larger limbs, while vireo nests are lower and hang between smaller branches of smaller trees. Higher nests may be parasitized less frequently. Briskie *et al.* [3] reported a decrease in parasitism rate as nest height increased in Yellow Warblers and Least Flycatchers at Delta Marsh, Manitoba. In New Mexico, Western Wood-pewees nest lower (3.6 m) and have higher parasitism rates (19%) [20] than we found in Colorado where pewees nested at an average height of 4.8 m and are rarely parasitized (<1%). However, Robinson [53] reported greater parasitism on higher nests in Illinois. Therefore we did not obtain support for the hypothesis that pewees are rarely parasitized because their nests are more concealed than vireo nests, but nest height might influence cowbird detection if cowbirds predominantly search lower in the canopy [6].

Breeding Asynchrony

The timing of host egg laying and incubation may influence the availability of host nests to female cowbirds. Our study suggests that the temporal overlap in the breeding cycle of cowbirds and vireos facilitates the use of vireos as hosts, whereas the breeding asynchrony between cowbirds and pewees reduces the opportunities of the pewees being parasitized (Fig. 2). Vireos laid their first egg 13 days before pewees lay their first egg, such that cowbirds passed their egg-laying peak before pewees initiated their clutches. Cowbirds have many hosts to choose from in the ponderosa pine forest of Boulder County, including Chipping Sparrow (*Spizella passerine*) [54], Western Tanager (*Piranga ludoviciana*) [55], Lesser Goldfinch (*Spinus psaltria*) [56], and Spotted Towhee (*Pipilo maculatus*) [57]. This study only focused on two primary and relatively abundant potential host species, therefore the timing of pewee nesting may overlap other potential hosts that are more suitable to raising cowbirds further diluting potential parasitism. Renesting following nest predation early in the breeding season may also increase the number of potential nests available to a female cowbird at the same time that pewee nests become available. However, these caveats cannot completely explain why nearly all pewee nests are unparasitized. Later nesting may provide a mechanism that reduces the threat of parasitism.

CONCLUSION

The Western Wood-pewee is a suitable cowbird host. They feed on insects, a diet appropriate for cowbird young. Their 14-day incubation period is within the range necessary for the 9-day incubation period of cowbirds. Curson *et al.* [28] and Ward and Smith [21] have shown that Western Wood-pewees can successfully fledge cowbird young, yet Western Wood-pewees are rarely parasitized in Colorado. In our study area Plumbeous Vireos are heavily parasitized while Western Wood-pewees are not, perhaps because of the

temporal asynchrony of egg-laying coupled with different species-specific foraging behaviors that characterize their pattern of nest attentiveness.

The temporal asynchrony in host breeding initially partitions hosts, favoring parasitism of vireos over pewees on our study site, which is then reinforced by host behavior such as nest attentiveness and aggression. This temporal disparity means that cowbirds need to focus their effort toward successfully parasitizing early nesters like vireos rather than late nesters like pewees so they can maximize the number of successful eggs laid and therefore maximize reproductive success. Vireos typically ranged farther from the nest area, presumably to glean insects, while the sally-hovering pewees typically stayed closer to their nests for longer periods of time. While both species are aggressive towards cowbirds, pewees are more likely to detect and attack nest-searching cowbirds because of where and how they forage. These results suggest that pewees are more likely than vireos to constitute an obstacle to an intruding cowbird than vireos. In conclusion, our results suggest that a temporal asynchrony in host availability sets a platform upon which other behavioral differences reinforce the cowbird's preference for vireos as a host.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflict of interest.

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