Are we adequately assessing the demographic impacts of harvesting for wild-sourced conservation translocations?

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Abstract
Translocation, the human-mediated movement of organisms from one area to another, is a popular tool in conservation management. Wild-caught individuals are more likely to persist following release than those sourced from captive breeding. However, this benefit of obtaining individuals from wild populations must be carefully weighed against the potential harm to the viability of source populations. In this structured review, we assess the peer-reviewed primary literature that addresses wild-sourced translocation programs. We aim to determine what proportion of studies make a priori estimates of the impact of harvesting on source populations, what proportion provide quantitative evidence of demographic trends in source populations following harvest, and which methods are being used to assess impacts of harvesting on source populations. Of 292 articles reviewed, we identified just 32 instances (11%) where impact on the source population was estimated. The proportion of studies that assess impacts on source populations in a given year has not increased over time. However, studies that make explicit a priori comparisons of alternative harvesting strategies are becoming more frequent. We propose a standardized framework for reporting on management of translocation source populations. Published summaries of wild-sourced translocations should include clear conservation goals, a description of the methods used to assess potential impact, an a priori justification based on evidence for the chosen harvesting strategy, an estimated timeline for recovery and a summary of postremoval population trends to assess the efficacy of a priori impact assessment. Routinely reporting impacts of harvesting on source populations will inform management when source sustainability is uncertain, improve transparency and increase the likelihood of successful conservation for many threatened species.

1 | INTRODUCTION

Much of biodiversity conservation contributes to one of two fundamental components: the preservation of existing biodiversity assets, or the restoration of those that have been degraded by human activity (Possingham, Bode, & Klein, 2015). While both approaches are important, preservation is typically considered the higher
priority (Benayas, Newton, Diaz, & Bullock, 2009; Dodds et al., 2008; Possingham et al., 2015). Restored ecosystems may take years or decades to begin providing desired biodiversity values, require significant financial investment, and yet often still exhibit lower levels of biodiversity than comparable preserved systems (Benayas et al., 2009; Dodds et al., 2008; Rohr, Bernhardt, Cadotte, & Clements, 2018). That is not to say that restoration is not important: it is (De Groot et al., 2013; Lindenmayer et al., 2012; Possingham et al., 2015). Rather, conservation practitioners should primarily seek to protect intact biodiversity assets while also engaging in complementary practices framed around restoration and recovery. Defined by the IUCN as “the human-mediated movement of living organisms from one area, with release in another,” translocation is such a management tool typically employed with goals of restoration or recovery (IUCN/SSC, 2013). Translocation is an overarching term that encompasses reintroduction (organisms are returned to an area within their indigenous range but from which they have become extirpated), augmentation (releases bolster at-risk extant populations), and conservation introduction (animals are introduced outside their indigenous range for some conservation benefit; IUCN/SSC, 2013; Seddon, Griffiths, Soorae, & Armstrong, 2014). The focal point of any translocation study is invariably the release population, but it is critical that recovery actions are not made at the expense of extant populations from which translocated individuals are sourced (Bain & French, 2009; Dimond & Armstrong, 2007).

As a popular tool leading to some highly publicized conservation success stories (e.g., Bolam et al., 2020; Greenfield, 2020; Lavery & Moseby, 2014), conservation translocation has received considerable research attention in recent decades (Berger-Tal, Blumstein, & Swaisgood, 2019; Fischer & Lindenmayer, 2000; Novak, Phelan, & Weber, 2021; Taylor et al., 2017). This has led to the establishment and ongoing curation of comprehensive best-practice guidelines. Against such guidelines, we can assess current practices, including those relating to the origin of translocated organisms (IUCN/SSC, 2013; Taylor et al., 2017). Usually a choice between wild-harvesting or captive breeding, the origin of translocated individuals can influence the success of a translocation as wild-sourced animals typically show higher survival than their captive-bred counterparts (Fischer & Lindenmayer, 2000; Rummel et al., 2016). Additionally, increasing the size of founder populations can increase the probability of ongoing persistence following release (Deredec & Courchamp, 2007; Fischer & Lindenmayer, 2000). Accordingly, using larger numbers of individuals from wild sources may be attractive for its likely enhancement of translocation success. Nonetheless, such an approach must be carefully weighed against the potential damage harvesting may cause to wild source populations (Armstrong & Wittmer, 2011). For this reason, the IUCN guidelines for reintroductions and other conservation translocations (IUCN/SSC, 2013) explicitly state that

“If removal of individuals or propagules from a source population causes a reduction in its viability in the short term, the translocation objectives should include balancing this with the expected gain in viability of the destination population, so that the species has a greater overall viability than without the translocation, within a stated time period.”

It is also typical that managers must provide regulatory bodies governing translocations in their region with evidence that source populations will not be negatively impacted in the long-term. For example, the Australian state of Victoria’s Threatened Fauna Translocation Evaluation Panel (2019) require managers to

“comment on the effect of removing individuals on the source population, including any demographic or genetic effects and whether the removal will affect the viability of the source population.”

Despite these recommendations, a clear framework for assessing demographic impacts on translocation source populations does not appear to be widely used.

Adaptive management is designed to aid decision-making in complex systems while providing an opportunity to increase knowledge of those systems (Williams, 2011). Adaptive management of commercially harvested game populations is common (Moa, Eriksen, & Nilsen, 2017; Ramsey et al., 2010), but do we apply the same level of rigor to conservation restoration? Under adaptive management, clear goals and quantifiable indicators of success are identified and predictive models are used to inform management actions (Lacy, 2019; Williams, 2011). The outcomes of management actions are carefully monitored and any knowledge gained is then used to update predictive modeling, in turn, informing future management actions in an iterative process (Williams, 2011). Sustainable harvesting models typically rely on the concept of density-dependent vital processes (Bakker & Doak, 2009; Brook & Bradshaw, 2006; Pöysä, Elmburg, Gunnarsson, Nummi, & Sjöberg, 2004), whereby a reduction in population density through harvesting can lead to increased fecundity and survival, ultimately resulting in a sustainable yield (Brook & Bradshaw, 2006; Saltz, 1998). Adaptive management has been applied
Effectively to the sustainable harvesting of translocation source populations. Dimond and Armstrong (2007) developed a priori harvest models, followed by post hoc monitoring to quantify and minimize harm to a translocation source population undergoing repeated harvesting. Harvest models were updated with monitoring data prior to any additional harvest events, ensuring the ongoing sustainability of their source population. The adaptive management process, as it applies to the management of wild translocation source populations, is summarized in Figure 1. Adaptive management—driven by high-quality ecological data—is considered the gold standard when it comes to managing threatened populations (Armstrong et al., 2007; Bakker & Doak, 2009; Rout et al., 2009). However, conservation happens at the coalface. The ecological data necessary for management can take years to collect and for species at the brink of extinction, decisions must frequently be made with imperfect knowledge of the focal system or species (Milner-Gulland et al., 2001). Life history traits, environmental variation, threatening processes, and many other factors are also likely to affect the data and analytical requirements to ensure sustainability (Colomer et al., 2019; Verdon et al., 2021). In light of these realities, it remains unclear to what degree critical analyses of the impact on source populations are implemented during translocation programs.

Structured reviews are commonly used to aid in objectively assessing practices across a specified timeframe (e.g., Berger-Tal et al., 2019; Taylor et al., 2017). In this structured review, we assess the peer-reviewed primary literature that addresses wild-sourced translocation programs. We aim to synthesize current practice and determine what proportion of studies make a priori estimates of the impact of harvesting. We assess what proportion provides quantitative evidence of population trends following harvest. We seek to determine the realized demographic impacts of harvesting for translocations on source populations. Finally, we outline a series of recommendations for translocation managers and their advisors, based on our findings.

2 | METHODS

2.1 | Search protocol

We searched for literature within the Web of Science citation search engine’s “Core Collection” and populated the topic field with the search term: “reintroduc* OR translocat*.” We limited our search to Web of Science categories “ecology,” “biodiversity conservation,” and “zoology” for the years 2010–2019 inclusive. We then manually screened all search results for relevance. We included literature with a focus on wild-sourced translocations of terrestrial vertebrate taxa where the motivation for translocation was conservation. Articles that investigated some aspect of a translocation that had already occurred and articles with a key aim of making a priori assessments of future translocations were included. Studies that assessed general conservation ecology or genetics of a specific taxon and then suggested translocation as a possible conservation strategy as a concluding remark were not included. To validate the comprehensiveness of our approach, we compiled a list of 20 relevant articles and checked whether they were captured by our search protocol (Table S1, Supporting Information). All test articles were captured by our search protocol. The distinction between a wild and captive population is not always well defined. For example, fenced wildlife reserves or small intensively managed islands could reasonably fit...
into either category. In such cases, we deferred to the author’s definition of the translocation source. We excluded literature where the focal translocation occurred prior to the year 2000 because our focus was on current best practices. We searched for literature published in the period 2010–2018 on 27th of February 2019 and searched for literature published in 2019 on the 29th of July 2020.

### 2.2 Analyses

Our initial search returned 3,509 publications, excluding duplicates. We read the title and abstract of each study and removed 2,184 studies that did not meet the criteria defined above. Alternative definitions of “translocation” (e.g., transportation of minerals such as soil or chromosomal translocation), focal taxa that did not meet the inclusion criteria and translocation of captive-reared taxa were common reasons for studies to be removed at this stage of filtering. We then downloaded the full text of the remaining 1,325 publications and assessed each against our inclusion criteria. An additional 1,033 studies were removed. Common reasons for exclusion at this step were, again, a focus on translocations of captive-reared individuals or where the primary motivation was mitigation of human-wildlife conflict. Through this process, we identified 292 relevant peer-reviewed studies for further analysis. We carefully read each article to determine whether and how the potential impact of translocation on source populations were addressed (Table 1). Studies that provided a source population estimate with no additional insight or justification for the potential impact of harvesting were not considered to have assessed source population impact. For each study, we also recorded the journal and year of publication, focal taxa, the focus of the article and the continent where the translocation took place. We used the IUCN Red List of threatened species to determine the threat status of focal species in each study at the time that each study was published (IUCN, 2020).

#### TABLE 1 Justification provided by authors for the harvesting strategy adopted in studies addressing wild-sourced conservation translocations

| Rationale used to justify harvesting for translocation | No. of studies |
|-------------------------------------------------------|----------------|
| Quantitative data indicating increase in population size at source site over a period of three or more years prior to the translocation occurring | 6 |
| Authors state that population has reached carrying capacity. In some cases this statement is supported by quantitative data indicating a plateauing demographic trend prior to translocation. In some cases this statement is supported by qualitative observations (e.g., lack of suitable nest sites, available food or breeding territories) | 7 |
| Harvesting limited to specified percentage of source population. In such cases the argument is made that harvesting a relatively small proportion of the source population will result in minimal harm but no evidence to support this argument is provided | 3 |
| Explicit modeling, using quantitative demographic data, of impacts to source population under alternative harvesting strategies prior to removal (as illustrated in Figure 1) | 8 |
| Subordinate nestlings were removed for translocation from the nest of a species in which siblicide is typical. No additional evidence provided to demonstrate that this approach did not lead to impact on the source population | 1 |
| No a priori estimate of impact but source population is monitored to track population trends postharvest | 6 |
| Source population managed adaptively with both a priori modeling of impact and post hoc monitoring (Figure 1) | 1 |
| Translocated individuals salvaged from area likely to be destroyed or degraded as a result of human impacts | 15 |

*Note: In total, 292 primary research articles published in the years 2010–2019 were assessed.*
increase with the threat status of the focal species. To test this, we used binomial regression with a logit link function, IUCN threat status as predictor variable and “whether or not impact at the translocation source site was addressed” as response variable. We compared group means using a post hoc Tukey test. We checked assumptions for all generalized linear models using simulated residuals with the “DHARMa” package and completed all analyses in the statistical environment R (Hartig, 2017; R Core Team, 2020). The genetic suitability of a source population is another important consideration for translocation managers (Houde, Garner, & Neff, 2015; Weeks et al., 2011). Likewise, it is important that harvesting does not reduce genetic diversity of source populations (Furlan et al., 2020). However, in this review we consider only demographic impacts on source populations.

2.3 Coverage of the literature

Our dataset included studies of active or planned translocations of 190 unique taxa including 23 reptiles, 75 mammals, 85 birds, and 7 amphibians. Studies originated from all over the world, though there was a clear bias toward wealthy regions with 34% of studies conducted in North America followed by 19% in New Zealand and the Pacific, 14% in western Europe, 12% in Australia, and fewer than 10% in each of central and southern America, eastern Europe, Africa, and Asia. Studies were published in 73 different peer-reviewed academic journals. Our dataset included studies with a wide range of key areas of focus: 26% investigated factors that may increase translocation success, 23% assessed destination population demographics, 20% made a priori assessments of translocation feasibility, 16% assessed population genetics of taxa that had undergone or were being considered for translocation, 15% assessed behavior of translocated taxa, 7% focused on assessment of competing management scenarios and fewer than 5% focused on each of physiology or morphology of translocated taxa, impacts of translocated taxa at the destination site, or basic ecology of the focal taxa. While not a systematic review, our structured review approach is consistent with other recent reviews that seek to provide representative insight into current translocation practice (e.g., Taylor et al., 2017).

3 RESULTS

Across 292 peer-reviewed publications documenting conservation translocations of terrestrial vertebrates, we identified only 32 (11%) cases where the impact of harvesting for translocation on the source population was assessed (Figure 2). In an additional 15 cases (5%) animals were “salvaged” from habitat directly threatened by human impacts. In 61 (21%) studies, the size of the source population was reported but any potential impact was not addressed. In 182 (63%) studies, no reference was made to potential impact on, or demographics of, translocation source populations. Two studies reported on reciprocal translocations between populations in attempts to bolster genetic diversity. In total, 52 reintroduction programs were addressed in two or more publications within our dataset. Of these, impact on source population was addressed in at least one publication for 12 (23%) translocation programs (19 publications). The proportion of translocation literature that assessed demographic impact on source populations did not change significantly from 2010 to 2019 ($Z_{1-289} = -0.024, p = .980$) (Figure 2a). However, for studies that explicitly compared alternative harvesting levels to identify an optimum harvesting
strategy there was a clear trend for these to be published more recently than those that undertook a more cursory assessment ($Z_{1-289} = -2.164, p = 0.031$). We detected a small, nonsignificant increase in the probability that impact at the source site would be addressed as IUCN threat status of the focal species increased from “Least Concern” to “Critically Endangered” (all $Z < 1.446$, all $p > 0.05$; Figure 3).

Several different rationales were used to justify removing individuals from translocation source populations (Table 1). The studies with greatest capacity to influence management used a priori population viability (PVA) modeling to assess the potential impact under multiple harvesting strategies. One study took this a step further, adopting an adaptive management approach to harvesting for translocation (see Box 1 for summary; Andreone et al., 2009).

4 | DISCUSSION

Despite the widespread implementation of translocation as a conservation management tool, we demonstrate that studies providing quantitative evidence of the impact of harvesting from wild source populations remain rare in terrestrial vertebrate translocations. A small subset of studies comprehensively report on population demographics across both source and release populations while providing explicit comparisons of alternative harvesting strategies. Such studies have become more frequent in recent years but still comprise only a small proportion of the translocation literature. Given that protection and restoration are fundamental goals of conservation translocation programs, it is essential that practitioners provide quantitative evidence that such initiatives result in a net positive effect across source and release populations (IUCN/SSC, 2013). The inherent risk of ignoring potential harvesting impact has been brought into focus by Margalida, Colomer, Oro, Arlettaz, and Donazar (2015) who reported that of 57 modeled competing strategies for harvesting of bearded vultures—Gypaetus barbatus—for translocation, 77% resulted in source population decline.

The need for conservation management supported by science that explicitly compares alternative management strategies has long been emphasized (Sutherland, Pullin, Dolman, & Knight, 2004; Taylor et al., 2017). In our sample of 292 papers, only the nine studies that adopted an a priori modeling approach were able to assess impact under different levels of harvesting. By contrast, 283 of these papers presented no quantitative evidence to suggest that the level of harvesting chosen was the optimum available strategy. As well as allowing managers to identify optimum harvesting strategies and minimize impacts from the outset, harvesting models provide a benchmark for comparison with the results of post-removal monitoring, thus providing the foundations for adaptive management (Armstrong et al., 2007; Rout et al., 2009).

Some managers have sought to harvest individuals for translocation without any reduction in the natural size of source populations (Ferrer et al., 2014). When populations are small, the risks associated with removing individuals for translocation may be exacerbated by inbreeding depression, genetic drift, or demographic stochasticity (Deredec & Courchamp, 2007; Norris, 2004). In such cases, acquiring individuals for translocation with no reduction in source population size may be particularly advantageous. Fecundity may be manipulated by artificially increasing carrying capacity through supplemental feeding (Ferrer et al., 2014; Ferrer, Morandini, Baguena, Newton, & Thompson, 2018; Richardson, Castro, Brunton, & Armstrong, 2013). This approach may allow harvesting from small populations, while minimizing risks associated with the declining population paradigm (Ferrer et al., 2014). One study in our dataset suggested that this approach might be a more economically viable source of individuals for translocation than captive breeding, while eliminating many common challenges of captive breeding programs, for example, expensive infrastructure, adaptation to captivity, and loss of predator avoidance behavior (Ferrer et al., 2014). The validity of the data and methods used to reach these conclusions have since been questioned in a critique that nonetheless did not reject the idea that artificially
bolstering fecundity may, in some cases, be cheaper than captive breeding as a source for translocations (Margalida et al., 2017). While further case studies may be required to demonstrate its effectiveness, artificially bolstering vital rates or carrying capacity of wild source populations may be a useful tool for minimizing the impact of harvesting in some translocation programs.

There are many scenarios where the requirement to report on translocation source population demographics may seem overzealous. A translocated species may not itself be of broad conservation concern, with harvesting carried out from large and demographically robust populations. In some scenarios, re-wilding or restoring ecosystem processes may be the primary conservation goal in a translocation program (e.g., Baker, Gordon, & Bode, 2017; Green et al., 2018; Perino et al., 2019). For example, Elk Island National Park, Canada, has been a source for wapiti—*Cervus canadensis*—reintroductions into various parts of North America for several decades (e.g., Muller et al., 2018; Ryckman, Rosatte, McIntosh, Hamr, & Jenkins, 2010). Wapiti are abundant in this reserve and number over 1 million globally (Brook

**BOX 1** A sustainable approach to harvesting the Endangered Apennine yellow-bellied toad

The Apennine subspecies of the European yellow-bellied toad—*Bombina variegata pachypus*—is listed as ‘Endangered’ in the IUCN’s red list of threatened species as a result of significant range reduction and population declines over the past 30 years (Andreone et al., 2009). In 2015, a program was initiated with the aim of reintroducing this species to restored habitats within its historic range (Canessa et al. 2019). A small and vulnerable source population meant that from the outset this project was carried out with the explicit aim of minimising negative impacts of harvesting. Three translocation strategies were considered: captive breeding, involving the removal of a small number of pairs which would become founders for a captive population and provide a small number of sub-adults seasonally for translocation; ‘head-starting’, involving the removal of eggs from the wild source population to be raised in captivity and then released at the metamorphos stage; and finally, a direct translocation of eggs from the source site to the release site. The authors built a quantitative model of the system and simulated population trajectories at source and release sites under each competing management strategy. Initially, all three strategies were implemented in parallel while monitoring continued across source and release sites. The knowledge gained during the first season of translocations was used to update simulations of future releases. Head-starting was identified as an optimum strategy after two seasons and was adopted for subsequent translocations. The number of juveniles detected at the source population in the two seasons following harvesting events were in the upper range observed since monitoring of this source population began in 2010, suggesting that harvesting was not having a negative impact.

This case study is a comprehensive example of the ideal management of a translocation source population. Canessa et al. (2019) explicitly consider the potential impact of harvesting from source populations, compare alternative management strategies using *a priori* modelling and justify their management decisions using quantitative evidence. They provide a detailed summary of their adaptive management process to aid other researchers in adopting a similar approach. Critically, they demonstrate the efficacy of pre-removal impact assessments using monitoring data.
et al., 2018). It is unlikely harvesting for translocation poses a serious threat to this species. Similarly, some species have become model examples for studying translocation practice. Island translocations of small passerines in and around New Zealand are routine and managers are among leaders in the field of translocation science. For such species, source and release populations may be small but have been intensively monitored for several decades (e.g., Armstrong et al., 2017; Miskelly & Powlesland, 2013; Parlato & Armstrong, 2018). For those actively involved in management, any impact on source populations would, very reasonably, be considered negligible due to the history of sustainably harvesting from these populations. In both of these examples, a detailed description of harvesting method with rigorous justification for management decisions may not be perceived as beneficial from the perspective of translocation managers on-ground. However, a standard framework around reporting would help capture the confidence in such management strategies while providing transparency and highlighting useful methods for managers working in other systems.

Here we focus solely on the management of translocation source populations. In practice, conservation decisions are made in settings with multiple interacting management goals. Persistence of the release population is typically an overarching goal of any translocation while logistical and financial constraints often influence decision-making (Dimond & Armstrong, 2007; McDonald-Madden, Chades, McCarthy, Linkie, & Possingham, 2011). Increasing the number of founders has been demonstrated to increase the probability of success when establishing new populations through translocation (Fischer & Lindenmayer, 2000). When a parallel management goal is to minimize impact associated with obtaining those founders, there is an obvious conflict of objectives. For optimum conservation outcomes, managers must consider the trade-offs between establishing or bolstering destination populations and minimizing impacts on source populations while operating within logistical and budgetary limitations.

To ensure the sustainable and transparent management of translocation source populations, we recommend the following approach. Prior to implementing a translocation program, managers should make an initial assessment of the likelihood and magnitude of negatively impacting source populations. If focal taxa are considered “least concern” by the IUCN red list and translocation managers can provide explicit prima facie justification that it is reasonable to expect little impact of harvesting, then additional assessment may not be required. In such cases, managers should provide rationale for this assessment in any published translocation summary. For any taxa that do not meet these two criteria, managers should identify quantifiable goals for minimizing impacts on source populations and for measuring recovery following harvesting. Quantitative evidence should be used to make an a priori assessment of the impact of removing individuals from wild populations. A range of scenarios should be considered to ensure that the best possible harvesting strategy is identified. Managers should provide a timeline for recovering populations to return to a preremoval state. In most cases, such a timeline may be achieved using a population modeling approach (e.g., see case study in Box 1; Andreone et al., 2009). Clearly, the demographics of the source population must be well-understood prior to a translocation taking place if they are to be used as a meaningful control against which recovery can be judged. These recommendations largely mirror those made by other active practitioners (Canessa et al., 2019; Dimond & Armstrong, 2007; Lacy, 2019; Taylor et al., 2017) and the IUCN (IUCN/SSC, 2013). However, we have shown here empirically that the following points are rarely addressed. First, source populations must be monitored following harvest to assess the efficacy of pre-removal impact assessments and to demonstrate population recovery. This step is particularly important if populations are to undergo multiple harvesting events, and is a requirement for adaptive management. Second, all publications documenting conservation translocations should address the following with regard to management of source populations:

1. What quantitative targets have been set to minimize impacts and track recovery?
2. What proportion of the population is to be harvested (including a breakdown of life-history stages if relevant)?
3. What methods are being used to assess demographic impacts?
4. Why is the implemented harvesting strategy the most preferred option?
5. What was the a priori projected timeline of recovery for the population undergoing harvest?
6. Did the population recover from harvesting? How does the rate of recovery compare with pre-removal assessment? (see point e)

In some cases multiple publications investigate different aspects of the same translocation program (e.g., Bennett et al., 2013; Bennett, Doerr, Doerr, Manning, & Lindenmayer, 2012; Ferrer et al., 2014; Ferrer et al., 2018). In such cases, at least one study should address the points above in regard to management of source populations, and subsequent publications should reference this.
5 | CONCLUSION

To reduce risk of overharvesting, we recommend that demographic impacts on translocation source populations be routinely estimated a priori and reported. Recovery following harvest should be monitored to ensure the sustainability of the source population and, in scenarios with multiple harvest events, to inform adaptive management. Methods for a priori assessment of source populations that formally quantify impact and provide a critical assessment of alternative management options should be prioritized over qualitative or circumstantial estimates of sustainability. Several high-quality case studies have been published illustrating the importance of, and appropriate methods for, sustainable harvesting of translocation source populations. Despite this, just 11% of studies in our sample provided a justification for removal of individuals from source populations. Routinely reporting impacts of harvesting on source populations will inform management when source sustainability is uncertain, improve transparency and increase the likelihood of ongoing persistence of the increasing numbers of threatened species offered a lifeline through translocation programs.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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